Introduction to
World
Vegetation

SECOND EDITION

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Introductic
World Vegetation

Second edition

Preface to second edition

During the ten years since the first edition of this book, the twin disciplines of ecology and biogeography have made significant progress. In particular, knowledge of tropical world vegetation has advanced enormously as the attention of the world's academic community has focused on the significance for the health of the planetary biosphere of these great biotic resources. In the new edition, therefore, advantage has been taken of this quantum leap in knowledge of tropical systems to illustrate principles from tropical examples. Great strides have also been made in the understanding of fundamental biological processes, for example, the realization that DNA incorporates mechanisms for self-generated changes as well as random ones, and these have been noted in the text. Moreover, whole new disciplines have recently emerged such as plant demography, which has provided important insights into the study of the population biology of land plants, and long-term micro-ecology studies, which are exemplified by the work of Harper and his colleagues at the University of Wales at Bangor. However, significant gaps remain in our knowledge of the world's vegetation and its processes. The detrital energy pathway, for example, which is so important to soil functioning and the life of the vegetation it supports, is still not well understood in the majority of the world's vegetation types. Also, even after decades of work and argument, the modelling of plant communities is not completely settled. In any case, even the basic inventory of the world's flora is far from comprehensive. (Given the current rates of destruction it may now never be so.)

Although the format of the book in two parts has been retained, opportunity has been taken to reshape and expand the text. The references have been extended, but the asterisked guide to reading and the short comments which proved so useful in the first edition have been kept. The author hopes that the new edition will provide a new generation of students beginning their higher education courses in ecology and biogeography with a reliable companion to these complex and fascinating subjects.

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PART 1

Environmental and ecological principles

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Land plants, evolution and geography

1.1 The classification of plants

From earliest times to the present day, human beings have paid close attention to the plant kingdom on Earth. The needs for food, shelter, clothing, medicines and even magical and religious practices have ensured that any society, whatever its cultural level, has had to take stock of the plant resources of the region it inhabited. Consequently, by the time of the European Renaissance, an enormous stock of plant lore had been accumulated around the world, and from the 16th century onwards this accumulated knowledge has been patiently sifted and codified by successive generations of botanical scientists. This process began in earnest in the early 16th century with the publication of the first floras, in particular those by the great French botanist, Charles de l'Ecluse (Clusius), who produced the *Rarorium Plantarum Historia*, a flora of Europe in 1601. At the same time, the botanical resources of other areas of the world were being actively explored and a constant stream of specimens for the field, garden and herbarium were beginning to arrive at the public and private centres of learned culture in Europe. Turkey, for example, provided at that time the anemone, tulip, hyacinth, lilac and horse chestnut, which still adorn our surburban streets and gardens today. This sudden quantum leap in botanical knowledge presented science with two linked problems: first, how to name all the plants so that their relationships and differences would be universally clear, and, secondly, how to order all the information so that relationships and differences could form the basis of sets of plant groups. Both problems were finally solved by the great Swedish botanist, Linnaeus, who in 1736 and 1737 introduced the binominal system (the Latin generic name followed by the specific name), which he applied to all plants and animals and which we still use 200 years later. Building on

earlier writings, he also introduced the system of ranked taxonomic
groupings: classes, orders, genera, species and varieties.

In the 200 years since Linnaeus' system was introduced and
generally adopted, further refinements have been added to it and we
now recognize additional affinities in classification, as can be seen
below in the full classification of the common dog rose:

Dog rose – *Rosa canina* Linnaeus; *Rosa systyla* Bastard.
Kingdom: Planta.
Subkingdom: Phanerogamae or Embryobionta.
Division: Magnoliophyta (also called Angiospermidae – flowering
plants).
Class: Magnoliatae (dicotyledonous plants).
Subclass: Rosidae.
Order: Rosales.
Suborder: Rosinae.
Family: Rosaceae.
Subfamily: Rosoideae.
Tribe: Roseae.
Genus: *Rosa.*
Species: Rosa canina L. or *Rosa systyla* Bast.

The above is an example of a phenetic classification which can be
empirically based on a variety of plant features such as flower
morphology, plant anatomy or embryo character. Today, such a
classification also takes into account chemical similarities and differ-
ences (see Harborne & Turner 1985, Bell & Evans 1978). The use of
plant anatomy for the purposes of classification has been expanded by
the advent of the scanning electron microscope, and such microscopic
features as pollen grain surfaces, textures and leaf epidermis can be
fully considered in the classificatory process. With the development
of the computer, the similarities and differences can now be more
effectively refined in numerical terms.

In contrast to phenetic classifications are those which are phy-
logenetic or evolutionary. Here the evidence of the most probable
evolutionary relationships between plants forms the basis of an
evolutionary family tree or *cladogram*. The *cladistics* of a plant, i.e.
the probable paths from its ancestry, can closely resemble or even be
the same as a tree diagram (*dendrogram*) based on a phenetic
classification. If this is so – and it rarely is – then the plants involved
are said to have a *patristic* relationship, i.e. a common ancestry.

Although cladistics could be the main way in which taxonomy

should develop to avoid the accusation that it is merely 'Baconian science' or data gathering without an adequate theoretical framework, the task is by no means easy. To establish adequately the evolution of any organism requires an adequate fossil record and this is rarely available.

Whatever the method employed to designate a plant species to a particular group, its name is conserved in the *International Code of Botanical Nomenclature*, a formidable volume which also incorporates the rules by which plant taxa may be legitimately named. The rule book is used in conjunction with preserved specimens kept at the major herbaria around the world. The rules by which a plant name may be changed or given to a new species are very strict and any author must adhere to these if a name change of an existing taxa is proposed or what is claimed as a new species is put forward.

1.2   Floras

The recording of the native plant stock of a region is probably the oldest systematic scientific endeavour of its kind. It can be traced back to at least the 14th century BC in Egypt, where a bas relief in the temple at Karnak records the flora of Syria. Also the Greek scholar, Theophrastus, towards the end of the 4th century BC, recorded at least 500 species of plants from around the eastern Mediterranean. In spite of all the effort of recording plants that has been undertaken in the last 300 years, the task of recording the world's flora is still far from complete. In the tropics, for example, where species richness in forests especially is much greater than in the temperate lands, the process of active discovery is still going on. Some temperate parts of the world, on the other hand, are now almost fully recorded. This is especially true of Europe, where, by a major collective effort in the last three decades, the *Flora Europaea* has been published in five volumes between 1954 and 1980, although only a little over 13000 species are involved. It will probably be many decades before any similar publication will be possible for other areas of the world where there are rich and complex floras. For example, the floras of Venezuela and Brazil are at least twice those of Europe. In the latter case, it is probably three to four times greater.

It is a sobering thought that the floras for these areas, when and if they are published, may well be either merely historical documents, given the rate of destruction in these lands, or inherently incomplete as the pressures of humankind on the land eliminate species before they can be recorded.

The methods used to record and store floristic data are still largely manual and – apart from those for South African floras – few of the major national botanical databanks have been converted to electronic data recording. This is understandable given the enormous quantities of data recorded and the magnitude of the task. For example, it is estimated that the total number of botanical specimens around the world is some 80000000, of which approximately half are stored in European countries.

Electronic data processing is nevertheless a valuable adjunct to plant study. The use of the computer for recording and storage of information has proved very valuable in producing relatively unbiased quantitative data for classification and recording of taxonomic information as well as for computer mapping.

It is in relation to the last function that electronic methods have come into their own. Some of the computer-produced maps have become very sophisticated documents indeed, giving a wealth of information about areal distribution as well as distinguishing – in some cases three-dimensionally – frequency and habitat data. At a large scale in Britain, for example, a computer-produced map for a county might distinguish by symbols woodland, hedgerow, scrub, acid heath and bog, grassland, waterside and marsh, water, roadsides and waste places, quarries and walls, and cultivated land.

Whether manual or electronic, the choice of map on which to record areal floristic data should conform to three basic principles (Stott 1981). First, the basic purpose of the map should govern its overall design – Who is the map designed to be used by? Is it meant as a research tool? Secondly, the degree and kind of generalization to which the available floristic information is to be subjected is governed by the scale of the map, so the choice of representation – dots, circles, shading, etc. – will be suited to the areal framework. Thirdly, the map should always reflect the quality of the information on which it is based.

The last principle is usually governed by the surveying method that has been employed to obtain the information. In botany and ecology, the surveying of the world's plant cover employs two main groups of methods. The first group answers the following question as accurately as possible: where exactly does a particular species occur? Answering this usually requires detailed survey, and the common method employed, at least in Europe, is to utilize a grid system, which is a systematic square-by-square recording of the presence or absence of a species. (The standard square is 10km^2 or 4mi^2 approximately). This, of course, requires a large number of surveyors but has the

advantage of being eminently suitable for adaptation to information retrieval systems. In Britain, the grid is further refined by its incorporation into much older established surveying units such as the Watsonian vice-counties first established in 1852 and modified in 1969.

The second method is to give a much more synoptic picture by sampling the vegetation itself. How many samples and how close the samples should be are questions to be decided empirically, having regard to the purpose for which the information is required. The two sampling methods most widely used are the quadrat and the transect. The former is very simple in principle: a four-sided area, its size (e.g. $50\,cm^2$, $1\,m^2$, several square kilometres) dependent on the kind of vegetation, is used to give as precise as possible a picture of such characteristics as species composition, abundance, etc., within it. The choice of position of the quadrat is also empirical – should it be random or regular? The square can be reduced to a single point quadrat with the plant material recorded at the points formed by pins suspended from the quadrat frame, or intersections of a grid of strings across it.

The continental (Zuricho-Montpellier or Braun-Blanquet) school of phytosociology employs a more severely logical surveying unit known as the *relevé*. This is related to a concept favoured by this school that there is a minimum area needed for a plant community to reach its full expression. For the vegetation types of Europe the relevés are semi-standard areas which have been determined by close study of a number of examples (see Sec. 7.4).

The transect method involves sampling along a line, the direction, length of line and the sampling interval being determined subjectively to suit the nature of the vegetation type and its change over space.

The raw field data that these sampling methods yield can be subjected to a wide variety of analytical techniques to discover underlying ecological and phytosociological relationships, and the reader will find an account of these in Chapter 7.

1.3 The study of geographical pattern in the world's flora

The varied distribution patterns of plants and the vegetation they compose have occupied the attention of botanists from the early 19th century. The two main lines of investigation were established at that time and may be exemplified by the focus of interest of two of the leading scientists in the field.

On the one hand, Alexander von Humboldt in 1802 was impressed by the way in which the plant cover of the Earth could produce vegetation of a similar appearance (*physiognomy*) although composed of genera and species of widely different types. His work was followed up in the later decades of the century by the famous German botanists, Drude, Engler and Schimper. The last-named's copiously illustrated account of the world's vegetation types with its emphasis on physiological response, published in 1893, firmly placed vegetation study on a scientific basis.

On the other hand, Sir Joseph Hooker in the 1840s pointed to the need for explanation of the occurrence around the world of the same plant taxa often separated by thousands of miles of ocean. Workers who took up this challenge include the Swiss, de Candolle, who published his *Géographie botanique raisonnée* in 1855, and the American, Asa Gray, with his scientifically rigorous studies of the comparative floras of North America and Japan.

The search for theories to account for the geographical patterns in the world's flora and vegetation has been actively pursued to the present day. New theories have constantly been developed as each new discovery in the allied fields of the other Earth sciences and biology add new dimensions to old problems. Although there is some confusion of terminology between the various branches of plant geographical study, the line of vegetation study has now been largely subsumed into the wider field of ecology. The line begun by Hooker is still recognized by many as 'plant geography'. Both aspects in some authors' views might be placed together under the heading 'biogeography'.

1.4   The development of the plant kingdom on land

In the total span of life on Earth (probably between 3000 and 3500 million years) plants have clothed the land abundantly for only some 400 million years. Their relatively late evolution indicates the difficulties presented by the land environment in terms of feeding, support and reproduction problems. One has only to compare the relative simplicity of seaweeds with the complex adaptive features of land plants to see how many evolutionary changes in external morphology, internal anatomy and life-history have been encouraged by the land environment (Fig. 1.1). Not that all the problems were solved at once. Figure 1.2 indicates the successive stages that have occurred over 400 million years or so. The logic of this evolutionary story is
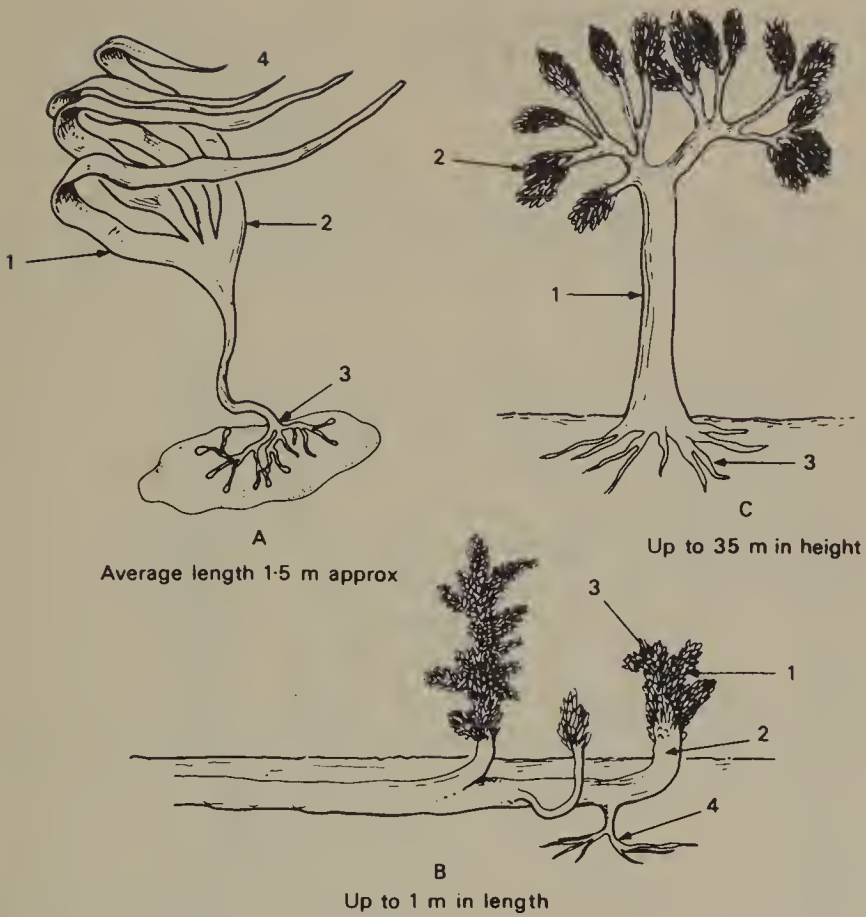
Figure 1.1 Morphological adaptations encouraged by the land habitat. (A) A modern seaweed (oarweed): (1) simple, relatively unspecialized form; (2) support provided by water with direct diffusion to all parts of water, light and nutrients; (3) no true roots, instead a simple anchorage by a 'holdfast'; (4) reproduction by free-swimming gametes released into the surrounding water and dispersed by currents. (B) *Asteroxylon*, a simple Devonian vascular plant: (1) leaf-like appendages for photosynthesis; (2) stem-like organ with vascular tissue transporting water and nutrients; (3) specialized spore-bearing organs; (4) root-like appendages with limited ability to absorb water and nutrients. (C) *Lepidodendron*, an Upper Carboniferous lycopod tree: (1) division into parts with specialized functions; (2) branches bear simple leaves and spore-producing organs; (3) true roots adapted to support and absorption of water and nutrients.

much more apparent than real, however. From Figure 1.2 it can be seen (a) that there are a number of extinct groups, shown by the lines ending in a cross, and (b) that the evolutionary steps are rather halting. Thus, the rise to dominance of the flowering plants occurred only during the Cretaceous period some 135 million years ago. As to why they should then have rapidly 'taken over the world' is, as Darwin said, 'an abominable mystery'. Their success certainly did not
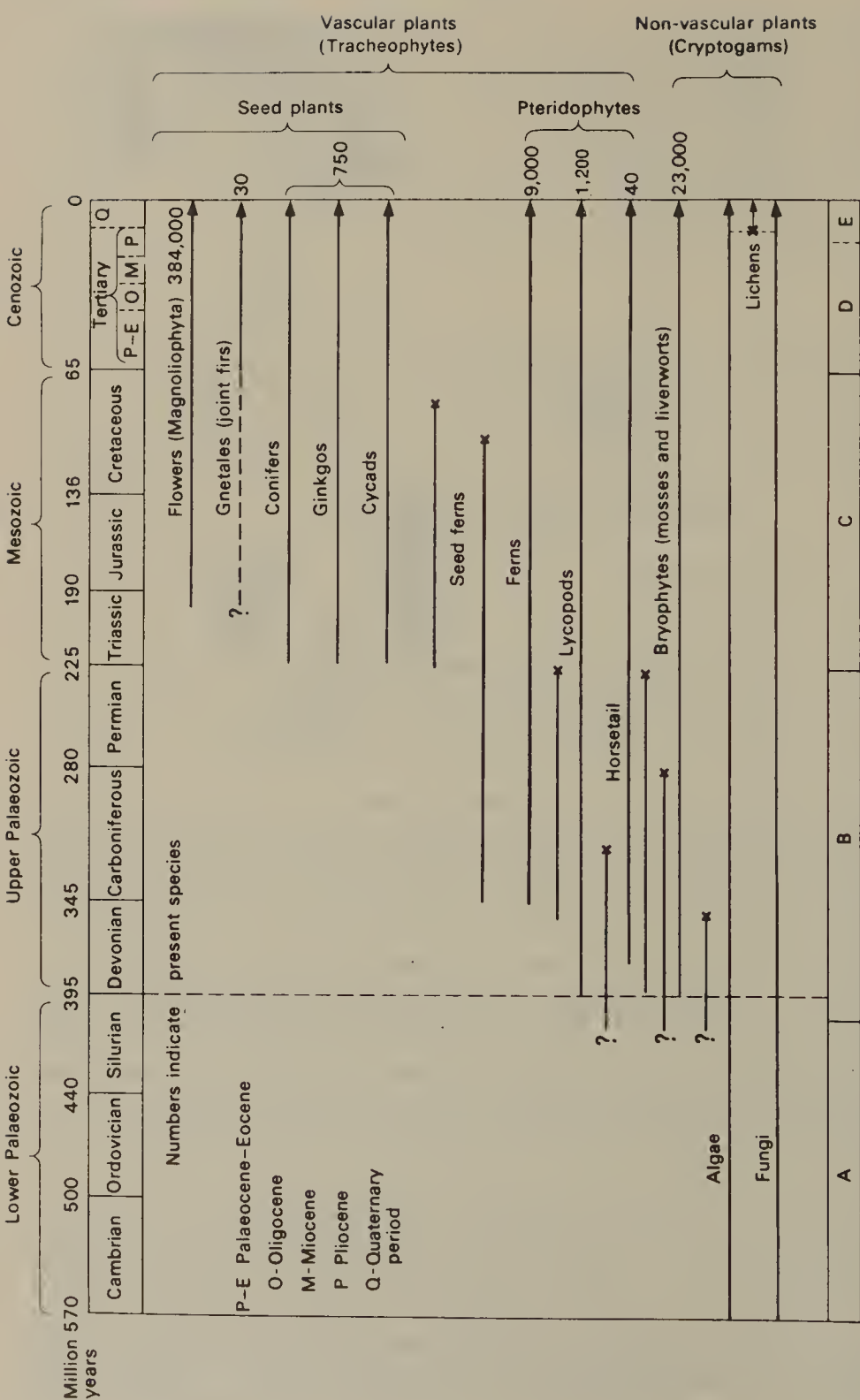
Figure 1.2 The evolution of the major plant groups. (A) Primitive land plants, mainly green algae in a few well-watered locations. (B) First forests with tree-sized plants during the Devonian period developing to luxuriant forests in the Carboniferous. (C) Fairly uniform forests dominated by conifers and cycads reaching peak during the Jurassic. (D) Forests dominated by flowering plants. (E) Appearance of widespread grasslands.

eliminate the more primitive groups. The mosses, liverworts, ferns and conifers, for example, seem to have survived quite well in spite of the lack of reproductive systems as sophisticated as those of the flowers.

How then can we account for these apparent anomalies in the evolutionary story? The simple answer is that we cannot do so completely. We really know very little as to why some groups succeed while others are extinguished, nor do we know why this seems to happen irregularly.

Various authors have proposed modifications to the current neo-Darwinian model based on reinterpretations of the fossil record. On the other hand, there are those theories sometimes called 'punctuated equilibrium' theories which attempt to show that evolution seems to occur in relatively short, sharp bursts separated by long intervals of apparent evolutionary stability. In this model, the rise of the flowering plants in the Lower Cretaceous could be just such a burst. On the other hand, extinctions, so long accepted as simply a corollary of biotic competition in evolution, have had much more attention paid to them in recent times. For example, Sepkoski (1983) claimed to have discovered a 26 million year rhythm of extinctions in the fossil record, but it is not yet clear (a) whether this rhythm is real or (b) whether the extinction rhythm can be correlated with the bursts of evolutionary activity. In any case, Kitchell and Pena (1984) have shown also that, whether or not a rhythm exists, the *slope* of extinctions during the time since the Cambrian has remained constant overall whereas the stability of the biotic system has increased (see also Raup & Sepkoski 1986).

Other authors have also identified extinction nexuses in the geological record (see Fig. 1.3) and derived further modifications of evolutionary theory from it. Hallam (1984), for example, suggests that evolution is essentially an interplay between extinction and radiation, and it is only when extinction allows radiation to take place that significant evolutionary changes can occur. Certainly, it is clear that flowering plants contain significant reserves of genetic material which only changed environmental conditions allow them to reveal. For Hallam, then, the first-order control of the evolutionary process is thus environmental change, not biotic competition as Darwin suggested. If this is the case, evidence of a major environmental change such as the marine transgression shown in Figure 1.3 would be expected to coincide with the rise of the flowering plants. However, the evolution of flowering plants appear to have progressed smoothly across the Mesozoic/Cenozoic boundary, the midpoint of angiosperm

Figure 1.3 Variation in world sea levels from the Cambrian onwards and major extinction episodes. R – major extinction of reptiles. (After Vail and Hardenbol (1979), Hallam (1984).)

evolution, and on through the Tertiary period. This may mean that the model is inapplicable or that our knowledge is incomplete. For example, at the Cretaceous/Palaeocene boundary, evidence has been found in many parts of the world of an anomalous contamination of sediments by the element iridium. This has been suggested as indicating that at that time the Earth collided with a huge meterorite, and the many extinctions that mark the boundary of the Mesozoic and Cenozoic have been ascribed by some geologists to the consequent disturbances of the Earth's atmosphere and oceans that followed this catastrophic event. (The mysterious extinction of the dinosaurs is the most striking, of course, although there is good evidence that they had been in decline for a considerable period before this.) Other geologists prefer to explain the iridium contamination as the result of volcanic action. It would be expected that, if such a major environmental disturbance had taken place, terrestrial plants would be extremely vulnerable and their fossil record at this level would show as striking changes, as does the animal record. The evidence is ambiguous, however. Most plant palaeontologists accept a smooth transition, but some (Nichols *et al.* 1986) have produced evidence that anomalies in the terrestrial plant record and iridium

content of rocks can be coincident. In south-central Saskatchewan, it has been shown that fern and angiosperm taxa were lost at this level, as many as 30% in the case of the latter, and that new angiosperm types became dominant in the Tertiary levels immediately above the iridium-contaminated layers. The workers also produced evidence to show that, if clamatic disturbance did take place, conditions quickly returned to a stable state. Also, research in the 1960s and 1970s has shown much of the earlier work on Tertiary flora to be misleading in any case, especially in the equating of fossil plants with recent genera (Müller 1981), so a further ambiguity is added to the story.

Harper (1983) has pointed out that the two views of evolution outlined above – 'biotic' control and 'environmental' control – were implied in the differences between Darwin and Wallace in the early days of evolutionary theorizing. (See also Section 7.3 for an account of Harper's own work on plant communities.)

Figure 1.4 models evolution as a train of pinions. As indicated, variations in the 'DNA drive' can be regular or random. The former kind are outlined in Section 1.7 below. However, in the case of random changes, some workers (Monod 1971, Johnson 1987) have emphasised thermal noise as the main cause of such variation.

The concept of thermal noise derives from the field of information theory. In any communication system where information is stored or transmitted in a form which can be affected by temperature, constant random motion of the materials composing the information or the transmitter will result in loss of coherence of the information. This
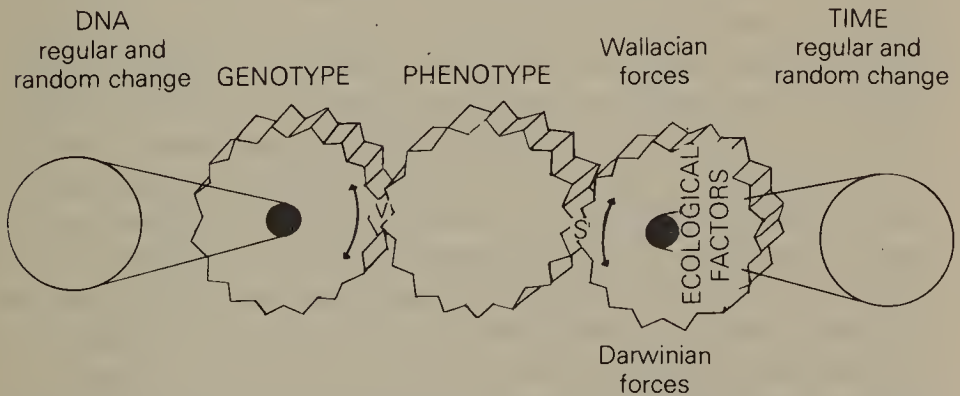
Figure 1.4   A model of the evolutionary process as a train of pinions. S – the process of selection. V – the genetic variations that determine the phenotype. As indicated, the evolutionary process can be 'driven' from either end so that the central pinion, the phenotype, is liable to alter its position *vis-à-vis* the genotype or ecological pinions at any time.

increased incoherence is described as noise. In all active biological systems where information is stored and messages transmitted in the form of macromolecules, many of the restless metabolic activities which are characteristic are concerned with counteracting this constant loss of information. When temperatures internal to living material reach a critical point (around 37°C (Johnson 1987)), the loss of information begins to exceed the capacity of metabolic processes to counter it. DNA is, of course, also subject to changes in its information content (**mutations**) through thermal noise and much of the mutated redundant information so created is preserved and inheritable. Monod (1971) expresses the relation of DNA to information change by likening it to a conservatory where the noise is preserved along with the music.

If this information theory approach is a correct analysis of the cause of most of the random additions to the DNA drive, it may be hypothesised that there are biogeographical implications for land plants. For example, it might be expected that environments which are subject to higher temperatures would be likely to generate more thermal noise-induced mutations, i.e. low latitude environments. As yet, however, the further implications of information theory remain to be explored in biology.

1.5   The evolution of geographical pattern in the world's flora

From the time when the flowering plants spread rapidly round the world to the present day, the plant cover of the world's land masses has never ceased to evolve. Mutations (changed inheritable characteristics) have emerged continuously and their survival and establishment has depended on the ecological circumstances prevailing at the time of their appearance. Climates have changed, often drastically; continents have shifted their positions, isolating some plant groups, joining others; new mountain barriers have arisen and new animal species have evolved. Thus the world today does not have a uniform flora: the thousands of species of plants are spread in a jumble of individual distribution patterns. However, it is not a completely haphazard jumble.

Major prehistoric environmental changes ('palaeoecological events'), like the splitting of a supercontinent or the advent of an ice age, tend to affect large areas simultaneously, so many species come to have greater or lesser coincidence in their distributions and we can

pick out major and minor regions where there is some coherence in the patterns. We can even draw maps generalizing these, as in Figure 1.5. Note that this is not a map of vegetation types but a map of the world's **flora**. The distinction between the two is important. Vegetation may be defined as the kind of plant cover in an area – forest, grassland, etc. – but the flora of an area is the sum total of all the plant species in it. Thus, although two floral regions (e.g. the Amazonian and West African forests) may be similar in vegetation because both are tropical forest of one kind or another, they might have little in common botanically and share only a relatively few genera. The unifying link is life-form and physiognomy.

The phenomenon of similar physiognomy in widely different assemblages of plant types, which Humboldt noted, is a result of the selective forces of the environment producing convergent evolution. The selective pressure of moisture availability in middle and low latitudes especially and of low temperatures in higher latitudes are such that these two factors are the fundamental keys to the understanding of both the distribution of much of the vegetational clothing of the land and its physiognomy.

To define a floral region of the scale of those in Figure 1.5, the botanist relies on the geographical distribution of plant genera. These are mapped individually, and from comparison of distributions a number of natural units emerge containing suites of genera that are distinctively characteristic of particular regions. These are then grouped at a higher level into kingdoms, which may have many fewer genera in common than those at a lower level. Thus Good (1974) lists only 250 genera as common to the Palaeotropical and Neotropical realms.

Not all authors are agreed as to the boundaries of the plant realms or to their number. The particular source shown, for example, has 38 divisions, eight more than many West European and American authors recognize. There is space here to give only brief details of the major realms. More complete accounts may be found in the standard texts, for example Good (1974) and Daubenmire (1978a). In their further reading, students may find it useful to note some of the terms employed by plant geographers. Floristic units are called *phytochoria*. A plant that is found in one phytochorion but is characteristic of another is said to be an *element* of the former. Taxa that occur in two or more phytochoria are called *polychoria* or *liaison taxa*. The degree of dissimilarity between phytochoria can be given a statistical basis by determination of what is called the *demarcation knot*, a quotient from 0% (identical flora) to 100% (no common taxa). So far, this has been
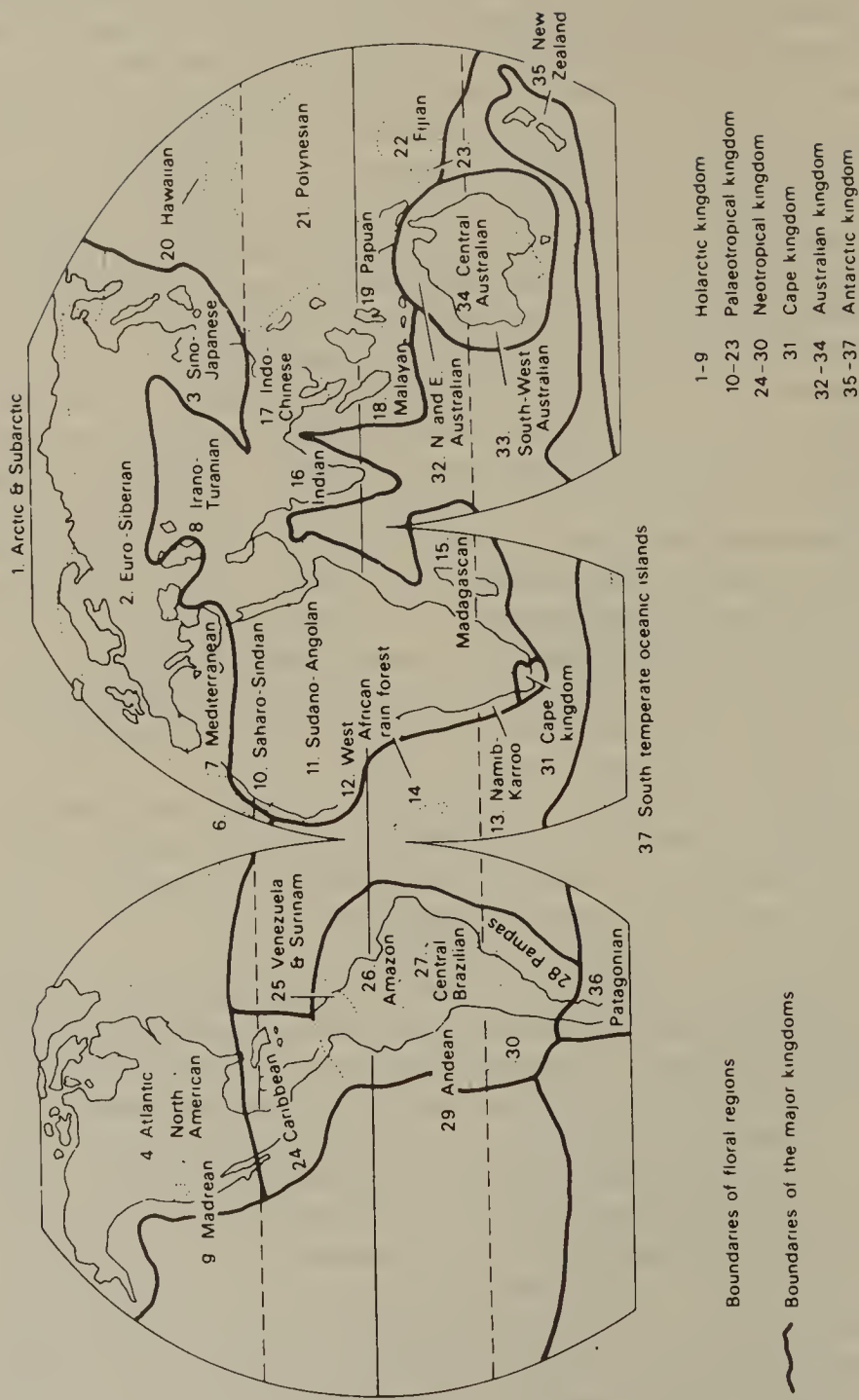
Figure 1.5 The world's floristic regions. (After Takhtajan (1969).)

1. Arctic & Subarctic
2. Euro-Siberian
3. Sino-Japanese
6.
7. Mediterranean
8. Irano-Turanian
9. Madrean
4. Atlantic North American
24. Caribbean
25. Venezuela & Surinam
26. Amazon
27. Central Brazilian
28. Pampas
29. Andean
30.
36.
Patagonian
10. Saharo-Sindian
11. Sudano-Angolan
12. West African rain forest
13. Namib-Karroo
14.
15. Madagascan
16. Indian
17. Indo-Chinese
18. Malayan
19. Papuan
20. Hawaiian
21. Polynesian
22. Fijian
23.
31. Cape kingdom
32. N and E. Australian
33. South-West Australian
34. Central Australian
35. New Zealand
37. South temperate oceanic islands

Boundaries of floral regions

Boundaries of the major kingdoms

1–9   Holarctic kingdom
10–23   Palaeotropical kingdom
24–30   Neotropical kingdom
31   Cape kingdom
32–34   Australian kingdom
35–37   Antarctic kingdom

applied completely only to the flora of the Pacific Basin, but some work has been done for the fern taxa of Europe. Phytochoria recognized below the level of the regions are *floral provinces* and below these *floral districts*.

The Holarctic floral realm

The mountain chains from the Atlas to the Himalayas form the southern boundary of this realm in Eurasia and particularly limit the southern extent of the conifers *Pinus* (pines), *Cedrus* (cedars) and *Abies* (firs). It is also the geographical northern limit of all but one type of palm (*Chamaerops* occurs in the Mediterranean Basin). In North America the mountains of Mexico mark the southern limit of firs and pines, and only two types of palms transgress the boundary into the northern continent – *Washingtona* in southern California and *Sabal* in Florida. The North American and Eurasian sections of the kingdom have many families and genera in common, pointing to a long period of common evolution. Thus the beech (*Fagus*), oak (*Quercus*), lime (*Tilia*) and ash (*Fraxinus*) genera have taxa that are widespread across North America and Eurasia; the hemlocks (*Tsuga* spp.) and hickories (*Carya* spp.) of North America, although not present in Europe, are represented as Pleistocene fossils.

Neotropical and Palaeotropical realms

Some families are represented more or less throughout the tropical realms (pantropical), such as *Palmae*, *Bombaceae*, *Podostemaceae*, *Rhizophoraceae*, *Rufflesiaceae* and *Theacaceae*, but there is a strongly marked difference between the flora of the Old and New Worlds. Thus Good (1974) lists only 250 genera common to South America and Africa. The dissimilarity in this case, unlike the similarity of the Old and New World Holarctic floras, suggests a long period of separate evolution.

Important naturally occurring families in the Neotropical realm are *Malphigiaceae*, *Collumelliaceae*, *Aextoxiaceae*, *Malesherbiaceae*, *Cannaceae*, *Bromiliaceae* and *Cactaceae*. Families endemic to the Palaeotropical realm include the *Pandamaceae* (screw-pines), *Nepenthaceae* (pitcher plants), *Lauraceae* (laurels) and *Melianthaceae*. The palms of the two kingdoms have a number of endemic genera, for example *Chameaedorea* and *Mauritia* in the New World and *Borassus*, *Raphia*, *Nipa* and *Areaca* in the Old World.

Cape, Australasian and Antarctic realms

Unlike the three great floristic kingdoms described above, there is less agreement amongst plant geographers as to whether the Cape, Australasian and Antarctic realms should be accorded separate status or, because of the affinities between them (such as families *Myrtaceae*, *Protaceae* and *Restionaceae*) and the presumed origin of the floras in one original land mass, whether they should form one greater Austral kingdom. For these reasons some authors prefer to distinguish the separate areas of the Austral kingdom as dominions or subkingdoms.

The occurrence of these southern floras, which have close affinities but are separated by thousands of miles of ocean and also by a continent covered with ice, exemplify in a most striking way the kind of problem to which plant geography addresses itself. How did they get there? What were their dispersal mechanisms? How were they affected by continental drift? Moreover, if a plant arrives at a new location, how does it establish itself? What evolutionary changes result in the process? What is the fossil evidence of past distributions? Have land bridges, if they existed, assisted dispersal?

If all the answers to these questions told a coherent story, it would be very satisfactory, but unfortunately they do not. Often, even within the same field of study, there may be serious conflicts of evidence. It is from these conflicts that the formulation of new theories in biogeography have arisen. The reader should note that biogeographical study is a notorious field for the generation of theory, often founded on very slim evidence indeed (for examples, see Schuster 1972).

1.6   Types of distribution pattern

There are no plant species that are common to all the regions in Figure 1.5. However, some types are very wide-ranging and these are divided into three groups: *arctic–alpine* plants, which are mainly perennial herbs; *temperate* plants, widely distributed in the wetter north temperate zone especially; and *pantropical* plants, almost universally weedy herbaceous species present throughout the tropics. Few areas are without restricted or **endemic** species, and several degrees of endemism are recognized. At one end of the scale are the broad endemics, which occur throughout a major region. At the other end are the narrow endemics, which are confined wthin very res-

tricted environmental and geographical limits. Some plants occur in two or more regions, which may be thousands of miles apart, and are called discontinuous or *disjunct* species (Thorne 1972). To find theories that account satisfactorily for many instances of this last kind of distribution is one of the most difficult problems in biogeography.

Most biogeographical theories must take account of three main sources of evidence. First, it is essential to know what a particular species needs to enable it to survive (a study known as *autecology*). Evidence generated by such a study may throw light on the conditions that might limit its spread. Secondly, the fossil record provides evidence of past distributions and what prehistoric environmental changes may have occurred to influence the patterns found today. Finally, by comparing the distributions of species for particular regions theories can be formulated that take account of correlations and discrepancies.

1.7 Plant genetics and plant distributions

The study of the environmental requirements of individual species in the herbarium and laboratory can often indicate the range of conditions that they can tolerate. This range is usually very different from the range of conditions that appears to limit them in nature. Plants reared in artificial environments repeatedly turn out to be surprisingly tolerant of conditions never found in their natural habitats. Why this should be so is not completely clear; it certainly implies considerably more genetic resources within the species than they usually display in their natural habitats. Part of the reason may be that plants seem to have much more complex inheritance mechanisms than animals, with much more frequent recombination and reassortment of genes during the formation of gametes (**meiosis**). Moreover, it is now realized that the molecular biology of plants is much more variable than that of animals. There is evidence that the nucleus, the mitochondria and the plastids in plant cells have distinct DNA systems that can play a part in the phenotypic expression of the plant. Moreover, it is estimated that almost half the flowering plants are *polyploid* in their genetics. This seems to arise most commonly from a plant with two sets of chromosomes (diploid) giving rise by irregular division to a plant with four sets of chromosomes (tetraploid). When pollination takes place, the tetraploid parent produces gametes with two sets of chromosomes, which, when

combined with a normal (haploid) gamete with one set of chromosomes, produces a triploid offspring.

The triploid offspring is usually unable to produce gametes compatible with either parent and thus is rendered sterile. The diploid and tetraploid parents can thereby become genetically isolated and rapid speciation may take place, although most authorities regard polyploidy as deleterious in general. Two examples, one assumed and one observed, will illustrate the importance of polyploidy in the process of speciation. In the North Island of New Zealand, the *Ranunculus* species *R.verticillata* and *R.insignis* both have 48 chromosomes but *R.nivicola* has 96 chromosomes and is assumed to have arisen as a result of doubling of the chromosome number (allopolyploidy) in a hybrid of the other two species. In Britain, a classic example is provided by the cord grass *Spartina*:

Spartina townsendii
(native to the British Isles)

Spartina alterniflora
(introduced to Southampton Water
from North America 1800–30)

sterile hybrid

allopolyploidy

(fertile plants observed 1890)

Spartina anglica
All present today
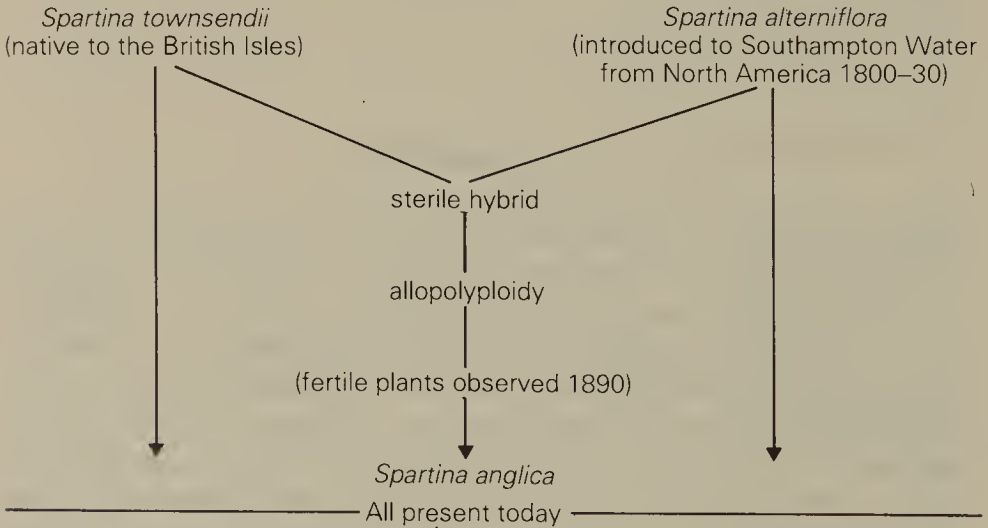
Some authors such as Lewin (1983) emphasize not only the genetic isolation aspect of polyploidy in speciation but also that polyploidy may confer novel abilities by which the potential to adapt to new environments is enhanced.

The hidden genetic resources of plants are astonishing, and when these are brought out in cultivation the number of true-breeding varieties that can be produced puts the achievements of animal breeders to shame. The chrysanthemum, for example, has at least 7000 varieties around the world, all descending from a single wild hybrid.

Generally, all wide-ranging types contain groups of local populations that form genetically distinct races. Many studies of the chromosome content of plants, hybridization (crossing) experiments and the classic method of growing plants from different regions

side-by-side under uniform conditions point to this. The local populations within these groups (called ecological races or **ecotypes**) are made up of individuals with similar environmental tolerances and are specialized to meet local environmental conditions.

In recent times, it has been discovered (Kimura 1979) that 'point changes' occur regularly on DNA molecules, i.e. living material incorporates a 'molecular clock'. This 'clock' ticks at different rates, slowly where DNA sites are of structural, **phenotypic** significance, and more rapidly at DNA sites with low functional significance. Thus, organisms can accumulate large quantities of redundant information, which may only be of significance in changed environmental circumstances. However, some workers, for example Wilson (1985), have suggested that, in animals at any rate, this accumulated information may produce an internal pressure to evolve, in addition to the Darwinian force of biotic competition and the Wallacian forces of environmental selective pressures. Most of the arguments in relation to molecular evolution have been derived from animal examples, but plants are known to contain large quantities of redundant genetic information and therefore may also be assumed to contain a 'molecular clock'. Whether 'internal pressure' to evolve can be demonstrated is not clear. (See Figure 1.4 for a diagrammatic model of the evolutionary process.)

The classic experiments demonstrating the existence of ecotypes were carried out by Turresson in Sweden in the 1920s on a variety of plants and since then new examples have constantly been demonstrated in many woody and herbaceous species in relation to the environmental variables of heat, light, moisture, soil chemistry and even man-made environmental factors. For example, the common grass, cock's foot (*Dactylis glomerata*), has been shown to possess distinct ecotypes, one adapted to grazed permanent pasture and one to annually mown hay meadows. Spoil heaps from metalliferous mining also often have a distinctive suite of ecotypes selected to tolerate extreme soil conditions. This has been studied in Britain particularly in relation to the common bent grass, *Agrostis tenuis* var. *Goginam* (Smith & Bradshaw 1979).

It must be pointed out, however, that not all plants that exhibit discernible morphological and physiological adaptations to environmental circumstances are necessarily genetically determined ecotypes. The series of experimental gardens maintained in California from the coast to the Sierra Nevada have shown that genetic ecotypes and plants of the same species without specified **genotypes** can appear identical. Thus, the latter (phenecotypes) exhibit the plasticity of the

genotype of the species as a whole. However, plasticity of this kind is not by any means possessed by all plants.

The presence of many ecological races in a species, combined with a wide tolerance range in individuals, results in a very broad tolerance range in the species as a whole. Thus the ability to disperse over many varied regions is enhanced. In fact, the ability to generate ecotypes seems to be a prerequisite for wide range in plants. Why some plants (e.g. the American prairie grasses) should have this ability while others seem genetically conservative and poorly fitted for wide dispersal is not well understood. Some narrow endemics may be newly evolved and may not have had time to disperse, e.g. the live oaks of California. Others – especially woody tropical species – seem to have changed little genetically for millions of years. Yet others, such as the Californian redwoods, are relict populations of species that were once much more widespread (see Fig. 2.1).

Moreover, it is possible that plants identified as distinct species in different parts of the world may have no genetic barriers to breeding. A good example is that of the plane species, *Platanus occidentalis*, a native of the Atlantic states of the USA, and the Eurasian type, *Platanus orientalis*, found in the Balkans and the Himalayan foothills. When grown together, they hybridize freely to produce a fully fertile viable variety, the London plane, *P.arcufolia* (*P.hybrida*).

1.8   Plant life-forms

The selective power of the environment is, of course, of much wider significance than the production of ecotypes. In land plants, it has produced a great variety of characteristic **life-forms**. Most of these were codified at the end of the 19th century by Carl Drude, who brought together the work of the scholars who followed von Humboldt. Alternative schemes have been proposed using, rather than the whole life-form, one or more major characteristics. One such scheme proposed by the Danish botanist, Runkiaer, in 1908 has a terminology still used in the literature and is based on the position of the perennating buds in relation to the ground surface and on leaf size. Both of these features are considered to relate to critical climatic factors. Runkiaer's classification is given in Table 1.1.

The major life-forms of Runkiaer have been shown to reflect the major environmental conditions in many parts of the world, but vegetation is never exactly all of one type of life-form. Thus, in the wet, hot tropics, 80–90% of the vegetation will be of phanerophytic

Table 1.1 Runkiaer's classification.

Plant form	Buds
Phanerophytes (plants with buds exposed on twigs above ground)	
Megaphanerophyte	+30 m
Mesophanerophyte	8–30 m
Microphanerophyte	2–8 m
Nanophanerophyte	25 cm–2 m
Therophytes survive unfavourable conditions as seeds	
Cryptophytes	
Chamaephytes	ground–25 cm
Geophytes	below ground
Helophytes	semi-aquatic
Hydrophytes	aquatic
Hemicryptophytes have their buds at ground level	
Leaf size categories	
leptophyll	up to 25 mm^2
nanophyll	25–225 mm^2
microphyll	225–2025 mm^2
mesophyll	2025–18 225 mm^2
nothophyll	2025–4500 mm^2
macrophyll	18 225–164 025 mm^2
megaphyll	>164 025 mm^2

life-form, and in the Arctic and in alpine tundras, Chamaephytes are the dominant characteristic life-form. But in both these areas, other life-forms can occur.

Most authors from von Humboldt onwards have recognized that the classification of life-forms is a very imprecise procedure, and there have been numerous additions to the terminology during the last 150 years. Where the terminology has proved useful, the terms have become generally adopted. Words like hygrophilous (plants in moist habitats) and xerophilous (plants in dry soils) introduced in 1849 are still used, as are mesophyte (plants adapted to moist atmospheric conditions), xerophyte (plants adapted to aridity) and tropophyte (deciduous plants alternating between moist and dry conditions) introduced in 1898. Almost 100 different life-forms were recognized by Drude when he codified much of the earlier work and defined the principal life-form types. These principal classes are: woody plants (classes 1, 3, 5 and 9), semi-woody plants (classes 2, 6 and 7), perennial herbs (classes 11, 12, 13 and 14), monocarpic herbs (class 16), water plants (classes 18 and 19) and thalloid plants (classes 17 and 20). The details of the classes are set out in Table 1.2.

The Drude classification of life-forms has been given a heightened

Table 1.2   Drude's classification.

Class/Division	Subdivision	Characteristics
1 crown trees	(a) evergreen hygromorphic to mesomorphic	thin bark; buds without scales; principal trees of tropical rainforest
	(b) tropophytic crown trees	seasonally deciduous; thick-barked trees; buds with scales; rain-green tropical forest; summer-green temperate trees
	(c) bottle stem trees	thick, flask-shaped trunk; mainly deciduous; seasonally dry tropics (the baobab, *Adamsonia digitata*, is a good example)
	(d) thorn trees	gnarled branches; wide-spreading crowns; thick bark; thorny twigs; some evergreen, some deciduous; semi-arid tropics and subtropics
	(e) sclerophyll trees	low to medium-height evergreens; small, hard or stiff leaves; thick bark with protected buds; characteristic of Mediterranean and similar climatic regimes
	(f) evergreen broad leaf	mesomorphic with firm, medium-sized, leathery leaves; thin bark; unprotected buds; tropical montane forests, e.g. those in Canary Islands
	(g) needle leaf trees	predominantly evergreen; coniferous; xeromorphic; thick bark and bud scales
	(h) scale leaf trees	leaves reduced to overlapping scales; semi-desert environments (*Cupressus* of conifers, tamarisk type in angiosperms)
	(i) succulent leaf trees	thick, glossy, tough-cuticled trees; low branching stems, often stilt roots; viviparous fruits; mangrove swamps
	(j) xylopod trees	underground water storage in swollen base of stem (xylopodium or lignotuber); dry north-east Brazil chaco forest
	(k) strangler trees	germinate as epiphytes, later extending roots to ground; capable of self-support; *Ficus* spp. of tropics and banyan types

Class/Division	Subdivision	Characteristics
2 tuft trees (distinct trunk trees, usually unbranched, terminating in a dense rosette of very large leaves; found in ferns, cycads, palms, screw-pines and a few genera of dicotyledons)	(a) hygromorphic tuft trees	10–20 m height; leaves soft, large, pinnate; tree ferns in frost-free shaded habitats mainly tropical (*Dicksonia antarctica* of Tasmania is a temperate version)
	(b) xeromorphic tuft trees	leaves divided either pinnate or fan-like, and firm, leathery to stiff; palms and palm ferns (cycads)
	(c) candle trees	single, unbranched trunk with a dense tuft-rosette of strap-like, leathery leaves from which a 'candle' axis arises bearing flowers; tropical, high-altitude types (giant lobelia of East Africa and *Espeletia* of high Andes)
	(d) grass tree types	fairly short trunk with forked branching, bearing terminal tufts of long, narrow, overhanging leaves (*Liliaceae* genera) or more profusely branched and taller (to 18 m) trees – *Yucca*, *Aloe* and some euphorbias
	(e) screw-pine types	stilt-rooted, hygromorphic, stout-trunked (branching) trees with long spirally arranged leaves at the top; *Pandanus* of tropical lowland and montane rainforest
	(f) succulent leaf tuft trees	short trunk with thick rosette of massive spade- or sword-like leaves; some species of *Aloe* (South Africa), *Yucca* (Central and North America) and *Puva* (South America)
	(g) false trunk trees	non-woody trees with dense, fibrous leaf sheaths supporting a crown of large, mesomorphic leaves; banana type of moist tropical forests
	(h) cane-trees	bamboo type, woody but no secondary thickening

Table 1.2   (contd)

Class/Division	Subdivision	Characteristics
3 lianas		long, branching-stemmed, climbing plants rooted in soil but not capable initially of self-support; subdivisions based on special attachment: (a) twining lianas, (b) root-climbers (ivy type), tendril climbers, scrambling lianas (wide-branching with hooks or spines to prevent slippage); the last is characteristic of lowland, wet tropics
4 epiphytes	taxonomically varied class germinating on trees and shrubs mostly with special means of attachment and many with water-gathering and storage organs	
5 shrubs	no district trunk; up to 5 m high	(a) evergreen, hygromorphic types with woody broad leaves and unprotected buds; wet tropics
		(b) seasonally deciduous tropophytic types with protected buds
		(c) mesomorphic, evergreen types with medium firm leaves; laurel types of moist subtropical mountains
		(d) scleromorphic, evergreen types with rigid, hard leaves; Mediterranean and semi-arid lands
		(e) xeromorphic ericoid types (heather family) with short, linear leaves inrolled to protect stomata
		(f) xeromorphic conifers with short, scale-like or needle-like leaves; juniper type
		(g) thorn shrubs; evergreen and deciduous; hot, arid lands except Australia
		(h) switch shrubs; leafless or minute scale-like leaves; tamarisk type
		(i) tola shrubs; resinous, aromatic and inflammable with hard, small- or needle-like leaves; puna regions of South America

Class/Division	Subdivision	Characteristics
		(j) succulent shrubs; succulent leaved shrubs of saltmarshes and deserts
		(k) xylopod shrubs; tuberous, water-storing underground stems
6 semi-shrubs	poorly wooded stems; annual or biennial shoots	(a) mesomorphic types with soft leaves on biennial stems; bramble type (*Rubus* spp.)
		(b) sage-leaved types; hairy, partially rolled leaves often grey-green; may be densely hairy; lavender type, *Salvia*, *Artemisia*; Mediterranean or semi-arid regions
7 succulents	plants over 20 cm with either succulent stems without leaves or rosette-leaved succulents with massive water-storing leaves; includes the *Cactaceae* (New World) and *Euphorbiaceae* (Old World) which have candelabra, columnar or shrubby forms; agave form has low stocky shoots with succulent, sword-like leaves	
8 dwarf succulents	usually below 0.5 m	wide variety of forms: globose-columnar, shrubby, branched trailing, leafy stem succulents, dwarf leaf succulents, pebble-like
9 dwarf shrubs	usually below 0.5 m	classes corresponding to 5(b), (d), (e), (f), (h), (j) and (k) plus creeping dwarf shrubs which can form a densely branched carpet a few centimetres above the soil in subalpine and arctic environments
10 cushion plant	densely packed, short branches forming a mound-like surface; can be herbaceous or woody; four classes are recognized: (a) hard cushion, (b) thorn cushion, (c) herb cushion and (d) moss cushion; the form is adapted to wind, low temperatures and drought	
11 giant herbs		hygromorphic, large-leaved, non-woody shade plants of the hot wet tropics; can reach 5 m
12 tussock herbs		perennials with buds above ground in tufts or on the stump-like base; includes (a) hygromorphic, broad-leaved, ferns with seasonal foliage, (b) tall tuft grasses (humid savanna types),

(contd)

Table 1.2 (contd)

Class/Division	Subdivision	Characteristics
12 tussock herbs (contd)		(c) bunch grasses with hard, inrolled leaves found in subtropical semi-arid lands, e.g. esparto grass (N. Africa) and spinifex (Australia); tussock grasses and sedges of wet, cool temperate lands
13 turf-dormant herbs		tropophytic plants with buds at ground level and aerial parts dying down in seasons with low temperatures; includes (a) rhubarb herbs, (b) stem herbs (annually renewed stems), (c) rosette herbs, (d) creeping herbs, (e) trailing herbs
14 underground perennials		herbs with underground organs from which aerial shoots develop; includes (a) bulb tuber plants, (b) rhizome herbs, (c) root parasites and saprophytes
15 winter annuals and biennials		herbs with one- or two-year lifespan; includes (a) winter annuals germinating in autumn and (b) biennials requiring two full growing seasons
16 ephemeral herbs and summer annuals		life-cycle completed in a short growing season; most of the shoot forms of the herbaceous perennials are represented
17 mat cryptogams		mosses, leafy liverworts, filmy ferns, thallose liverworts, and lichen mats (foliose, fructose and thallose types)
18 sudd plants		mostly grasses and sedges of tropical lakes and rivers; floating stems forming rafts
19 water herbs		entire form adapted to aquatic life; includes (a) floating leaf water herbs (rooted in sediment), (b) submersed water herbs (leaves not above water) and (c) natant water herbs not rooted in sediment
20 aquatic organisms		includes natant (floating) types and benthic types (wholly submerged)

significance through contemporary analytic methods. For example, Raven and Handley (1987) have shown that, viewed from the standpoint of cost–benefit analysis, plant life-forms from phytoplankton to large forest trees can be closely related to the balance between the needs for transport and the relation to water supply.

1.9   Life-cycle and life-form

The life-forms listed have evolved over a long period of geological time as evolutionary strategies to overcome particular problems of adaptation to environmental circumstances. The pioneers of vegetation study assumed that, by and large, life-form adaptation could be explained on the basis of physiological adaptation to climatic conditions. More recently, however, it has been recognized that adaptation to climate alone is not the sole factor in determining the life-form of plants. Equally important in the problem of adaptation is the life-history strategy that has resulted from the natural selection process.

Life-history not only implies the germination, growth, senescence and death of the individual but also the particular stage at which reproduction takes place, how many progeny are produced and what survival chances they have to reach reproductive maturity themselves. There is also the further question of what minimum population is necessary for a species to ensure its survival in a particular environment. Thus, for any life-form to have adaptive value, it must have evolved in conjunction with a life-cycle that is equally 'fit'.

'Fitness' of form and life-cycle is a term that, as Stearns (1977) points out, 'everyone understands but no one can define'. Two terms that have been widely applied in biology to 'fit' populations distinguish two main kinds of life-cycle. These are 'r selection' and 'K selection' (MacArthur & Wilson 1967). The term 'r selection' is generally used to imply that a population will be selected when it has early maturity, many offspring, a short life and large reproductive effort. On the other hand, 'K selection' implies that populations having late maturity, few and large offspring, a long life and small reproductive efforts will be favoured. The theory implies that genotypes that are r-selected will allocate greater resources to reproductive activity (r strategists), whereas K-selected genotypes (K strategists) will devote smaller proportions of resources to reproduction. The former will be more favoured in environments where death is density-independent and the latter in crowded environments where death is density-dependent.

The theory has been extremely influential and it has clear implications because of the disposition of internal resources to life-form. It received experimental confirmation in the work of Solbrig and Simpson (1974, 1977) on populations of dandelion (*Taraxacum officinale*). Within the study area, they discovered that the species population was made up of four distinctive phenotypic varieties in close proximity to each other. The four types were called A, B, C and D in the study. Under uniform experimental conditions, the type D seemed to be the best competitor from the vigour of its growth, but was noted to set fewer seeds than one of the others, type A. In the field conditions, type A (*r* strategist) was most frequent in the two plots that were mown. Type D (the *K* strategist) dominated only in the field plot that was in an undisturbed state.

This experiment shows, then, that we cannot simply divide up the list of life-forms into *r* and *K* strategy types. Whether a plant type is an *r* or *K* strategist will depend on the particular circumstances in which it finds itself. Also, as Stearns (1977) has pointed out, the variety of life-history strategies to be found in the plant kingdom cannot be explained solely as a result of competition of this kind. In particular, environmental uncertainty and predation have to be taken into account. Wilbur (1976), for example, showed the impact of these factors in relation to seven milkweed species (*Asclepias* spp.) in Michigan, demonstrating that environmental uncertainty and predation had greater or lesser effects from species to species. Thus, the success or failure of a plant type depends not only on the fitness of its life-form but also on its life-cycle strategy and on independent variables such as environmental uncertainty and predation. Nor are these all the factors; the reproductive pattern is also of significance, not only pollination and seed setting but also whether self- or cross-pollination is employed. This last is of particular importance in relation to geographical distribution. It has been noted for many decades that the peripheral populations (either geographically or ecologically) tend to be self-fertilized when compared to central populations. Indeed, amongst plants on continents, geographically marginal populations are almost always self-fertilized (Grant 1975). Also, in relation to reproduction, considerable evidence has been produced to show wide genetic variance for characters correlated with fertility. However, there is not a great deal of hard data to show how exactly this affects the population biology of plants (Solbrig 1980).

Since the publication of a review article by Harper and White (1974) pointing to the general lack of demographic studies in plant

biology akin to those on human and animal populations, the development of work of this kind has been very rapid and a distinct new discipline has resulted from it. This is called plant demography. One aspect of this subject (see also Ch. 7) is the relationship of adaptations of life-form structural units to the capacity of an individual to contribute to its population growth. Harper and White also point out that over time, with repeated growth and development cycles, the life-form becomes a reflection of the disposition of the energy resources available to a plant, which compensates for the various environmental, reproductive and competitive factors to which it may be subjected. How important this energy disposition is in relation to life-form and the reproductive strategy of the plant can be seen from figures published for the palm, *Astrocaryum mexicanum* (Sarukhan, 1980). An individual plant of this species around 120 years old will have deployed the following percentages of total dry matter over its lifetime in the pattern: roots and stump 5.5%, trunk 13.5%, leaves 46%, fruits 30% and reproductive accessories 5%. Few comparable figures exist for other woody species, temperate or tropical, although there are some for temperate herbaceous species (Bazzaz *et al.* 1987).

However, the energy expenditures quoted depart considerably from the general theoretical patterns proposed by earlier work (Ogden 1974), which suggested important senescence effects in perennial species in relation to reproductive effort. Virtually no senescence in reproductive capacity was detected in *Astrocaryum mexicanum*. It is clear that many further studies will be needed before firm conclusions as to the effect of the energy expenditure strategy over the lifetime of a plant can be seen in the context of the demography of a species as a whole (Reekie & Bazzaz 1987).

In conclusion, the life-forms we see in the world's vegetation are a result of a complex of selective forces, not only those such as temperature and moisture availability recognized by the pioneers of vegetation study, but also life-cycle pattern, population dynamics and reproductive strategies.

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2

The geological record and past distributions

2.1   The fossil record of past distributions

It is no accident that the most complete fossil records of land plants are in rocks that formed in shallow, swamp-filled lakes or lagoons, nor is it surprising that there are considerable gaps in the record. Also, both macrofossils (leaves, wood, bark, seeds, etc.) and micro-fossils (spores, pollen) present considerable problems of interpretation and identification. For example, they may have been carried long distances from their source and may mislead in the reconstruction of the flora of a particular area. Moreover, the primary stage of evolution in flowering plants seems to have been associated with insect rather than wind pollination. Thus, little pollen may have been released and species that may have been important may hardly be represented as fossils at all. In the mid-Cretaceous Dakota flora of Kansas, for example, over 200 angiosperm (flowering plant) types can be identified by macrofossils, but flower pollen represents only 5% of the total pollen types present (Axelrod 1970).

Plant fossils fall into five main types: impressions and casts; compressions; petrified remains; mummified remains; and pollen. The last two are significantly different from the others in that they represent the original material, which has not undergone some form of alteration during diagenesis and as a consequence can yield corre-spondingly greater amounts of information. Nevertheless, there are a variety of sophisticated techniques that can be applied to the first three fossil types to yield surprising amounts of data from the most unlikely material. For example, the advent of the scanning electron microscope has enabled considerable details of microscopic struc-tures to be recovered from well preserved casts and compressions, and the use of reflected or transmitted infra-red light can show details of the original surface of leaves. Unlike the taxonomic study of plants

currently extant, which relies on gross macroscopic features for identification, the palaeontologist has to rely on fragments, usually leaves and seed, for identification. (Since the early years of the century, the use of leaf cuticle, for example, has proved invaluable in tracing some of the main lines of both Mesozoic and Cenozoic botanical history.)

In spite of advances in technology, the most difficult problem in plant palaeontology, unlike animal palaeontology, is still that it has to deal largely with fragments rather than whole organisms. A trilobite, a gastropod, an ammonite or even a dinosaur can usually be fitted into a detailed sequence of forms representing a clear indication of the evolution of a particular animal type over time. However, some of the most important taxonomic characteristics of plants rarely occur together. For example, the leaves of oak can be traced from its oldest form, the genus *Quercophyllum* from the early Cretaceous of Virginia and Wyoming, USA, through to the Miocene, since when there appear to have been few changes; the leaves of oaks from eastern North America are almost indistinguishable from Miocene types, for example. Yet, without even a single specimen of acorn, no true evolutionary history of the genus can be written.

In spite of this and other difficulties, however, the history of the plant kingdom on land is now broadly known. The first traces of terrestrial plants are recorded in the rocks of Upper Silurian times, but it was in the Devonian period that the Earth's land surfaces received an extensive covering of primitive land plants, for example *Rhynia* and *Psilophytes*. By the end of the period, primitive gymnosperms and club mosses added to the vegetational variety, and in the subsequent Carboniferous period giant horsetails (*Calamites*), lepidodendroid species, tree ferns and true gymnosperms – the first seed plants – were evolved. The last, during the Upper Carboniferous (Pennsylvanian), included early conifers and *Cordaitales*. During the Mesozoic, cycadophytes (especially the order *Benettitales* and *Nilsoniales*) were added and many early members of the presently extant genera of ferns. Conifers were abundant, as were gingkophytes. During the Cretaceous period, the early angiosperms appeared and are represented in the fossil record by pollen that is ancestral to the dicotyledonous (*Magnoliidae*) and monocotyledonous (*Liliatae*) flowers. Differentiation of these plants, so the fossil record indicates, was rapid, so that by the Maastrichtian strata most of the major angiosperm taxa can be identified (Muller 1981). Up to this point, the flowers appear to have consisted of woody species, not herbaceous species, which seem to have evolved later, as did wind rather than

insect pollination. Differentiation proceeded throughout the Tertiary period of the Cenozoic, with a significant addition to the world's landscapes during the Oligocene of the first extensive grasslands. (Figure 2.1 gives an example of past and present ranges for two forest genera.)

The sudden appearance, spread and rise to dominance of the angiosperms is a long-standing mystery in the fossil record, leading some authors (for example Axelrod 1970) to suggest an origin as early as the Triassic, but there is general rejection of this hypothesis. Other authors have attempted to identify a 'cradle of origin' such as temperate montane 'islands' in areas of tropical and subtropical forests and the continent of Antarctica. None of these have been supported by fossil evidence. Yet other authors (Perry 1984) have taken a more uniformitarian approach, that is to draw conclusions from present evidence as to past conditions. The significance in the contemporary wet tropical forests of fruit-eating birds and large fruit for dispersal of many species has been noted, and it is suggested that the almost simultaneous evolution of fruit-eating birds and the spread of the flowering plants was the result of coevolution of both at the time. Also significant is the increased variety of pollinating insects in the Cretaceous record at the time of flowering plant evolution.

Whatever the answers are to this 'mystery', the evolution of any taxonomic group, not least the flowering plants, involves a spatial as well as a temporal dimension. New groups appear in particular localities, and whether they are represented eventually in other parts of the world depends on a variety of factors. As explained in Chapter 1, the Earth has by no means a uniform flora, and the explanations for this lack of uniformity can be sought in the interaction within geological time of the following factors:

(a) biotic factors specific to the evolutionary process;
(b) major palaeoecological events, especially continental drift-ing, mountain building and changing climates; and
(c) current climatic controls.

Increasingly important also are the effects of human beings moving plants either deliberately or accidentally around the world.

2.2 Biotic factors

Genotypic variability in plants and the different ways this can be
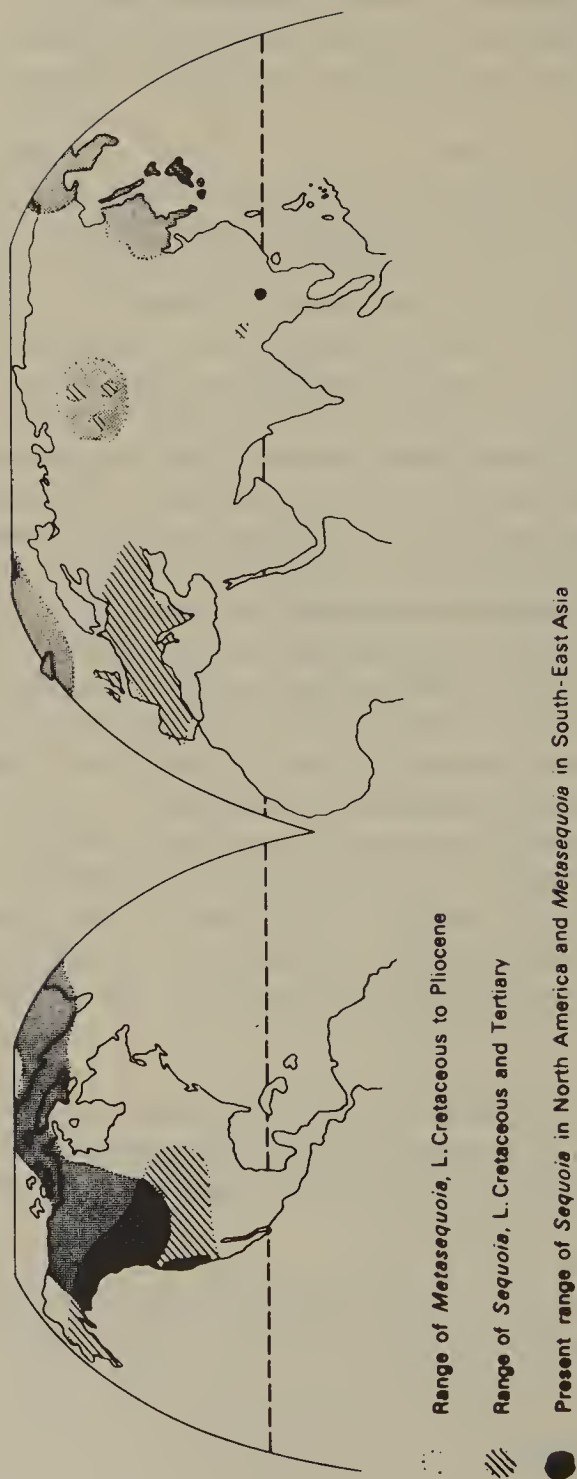
Figure 2.1   Past and present ranges of two Arcto-Tertiary forest genera. (From Schuster (1972), Frenzel (1968) and Takhtajan (1969).)

Range of *Metasequoia*, L. Cretaceous to Pliocene

Range of *Sequoia*, L. Cretaceous and Tertiary

Present range of *Sequoia* in North America and *Metasequoia* in South-East Asia

effected was discussed in Chapter 1. The forces of selection that impinge on the phenotypic expression of this genetic variation are of three kinds: directional, stabilizing and disruptive. Directional changes brought about by the environment can favour an optimum set of phenotypic characteristics, and those individuals expressing these will be favoured for survival, whereas those in which they are poorly expressed will not. Over the time, the latter will be eliminated, resulting in a shift of the average phenotype in the direction of the optimum for that environment. Cultivated crops and domesticated animals represent a forced version of this kind of selection.

The second kind of selective process may act to stabilize an optimum phenotype by eliminating variations as they appear. However, in variable environments this tendency towards a unitary, optimal type may be disrupted. To ensure success, there may be an advantage to the species in the generation of more than one optimal combination of genetically determined features. A simple example is presented by those plants where male and female are both optimal but act in a different yet related way.

The process of feature selection alone cannot produce new species. To produce the difference of gene frequencies, which is the essence of evolution, some kind of barrier to gene flow is required. The barriers may be entirely biotic, as in the case of polyploidy, or where asexual reproduction (*apomixis*) is of a kind where embryos are produced without fertilization. In this latter process, pure-breeding lines are produced; when cross-fertilization *does* take place, even though very rarely, a genetically distinct offspring can be produced. Should this offspring continue to reproduce predominantly by apomixis, then a new species may ultimately be produced. The hawkweeds (*Hieracum*), dandelions (*Taraxacum*) and blackberries (*Rubus*) have numerous varieties produced in this way. The tendency of the first group, for example, to produce new types meant that many years' work had to be done before a definitive account could be included in the standard flora of the British Isles.

Other barriers to reproduction include various kind of external and internal mechanisms. The former involve various means to prevent pollen and spores from reaching other species – flower shapes, colour and differential flowering times; the latter include the prevention of pollen germination by the stigma and the prevention of entry o the pollen tube to the ovary by the style. Also, hybrids in many taxa, should they occur in spite of these devices, may often display 'hybrid vigour' in the first generation but usually lose this two or three generations subsequently.

Although populations may be distributed over a common geographical area (*sympatric distribution*), they may nevertheless be separated ecologically. Ecological races (or ecotypes) are often the result of ecological isolation and over time always have the potential to develop into new species (see Sec. 1.6). The likelihood of this will be increased should significant geographical separation of ecotypic populations occur (Slatkin 1987).

Geographical barriers that prevent two or more populations of the same species from interbreeding and so lead to eventual speciation as the populations develop distinct genotypes are usually the result of geological or climatic changes. Although the timescale of the latter can be relatively rapid (see Ch. 8), both these 'Wallacian' selective pressures tend to act in the longer term in the process of speciation. Changes on a geological timescale that generate significant evolutionary developments are known as palaeoecological events.

2.3   Major Palaeoecological events: introduction

Two of the major insights in the Earth sciences of the last half century have been, first, the realization that the Earth's crust is composed of a series of large rotating plates (plate tectonics or continental drift theory) and, secondly, that almost all the world's surface environments have been profoundly affected by oscillations in the climate of the planet during the Cenozoic, culminating in the Pleistocene glaciations. Amongst the sciences that have had to look again at many long-standing problems in the light of these insights are plant geography and vegetational biogeography.

2.4   Continental drift and plant distributions

It was in the 1960s that the first real specific evidence was obtained to settle a question that had been speculated upon since the time of Francis Bacon. Bacon, in the early 17th century, noted an intriguing positive and negative correspondence of the coastal outlines of Africa and South America and speculated that they may have once been joined. By the 20th century, palaeontological and biogeographical evidence almost required that close connections should have once existed between parts of the world now widely separated. It was the discovery in the early 1960s that the ocean basins preserved a record laterally, not vertically as on the continents, of palaeomagnetic

changes that clinched the matter; the continents had indeed shifted and numerous maps of the reconstructed continental masses have since been published (see Fig. 2.2).

There is now general agreement that our current continental geography has been arrived at by the break-up of a single supercontinent called by the great German geologist, Alfred Wegener, *Pangaea*. This process began during the Jurassic period, when an Atlantic trough first appeared with the simultaneous rotation away from North America of South America and Africa. During late Jurassic and Cretaceous times, the two great continental segments (southern 'Gondwanaland' and northern 'Laurasia'), so created, themselves

A ⎫
B ⎬ Late Cretaceous Dinosaur Genera
C ⎭

Rifting ⎰ ① Late Cretaceous
        ⎱ ② Early Eocene

Probable transfer of Greenland to North American plate in early Eocene

• Eocene hot wet forest floras
○ Eocene warm temperate floras
■ Eocene cool temperate floras
□ Eocene 'arid' floras
Pm Eocene palm fossils

Note: Fossil floras positioned on reconstructed continents
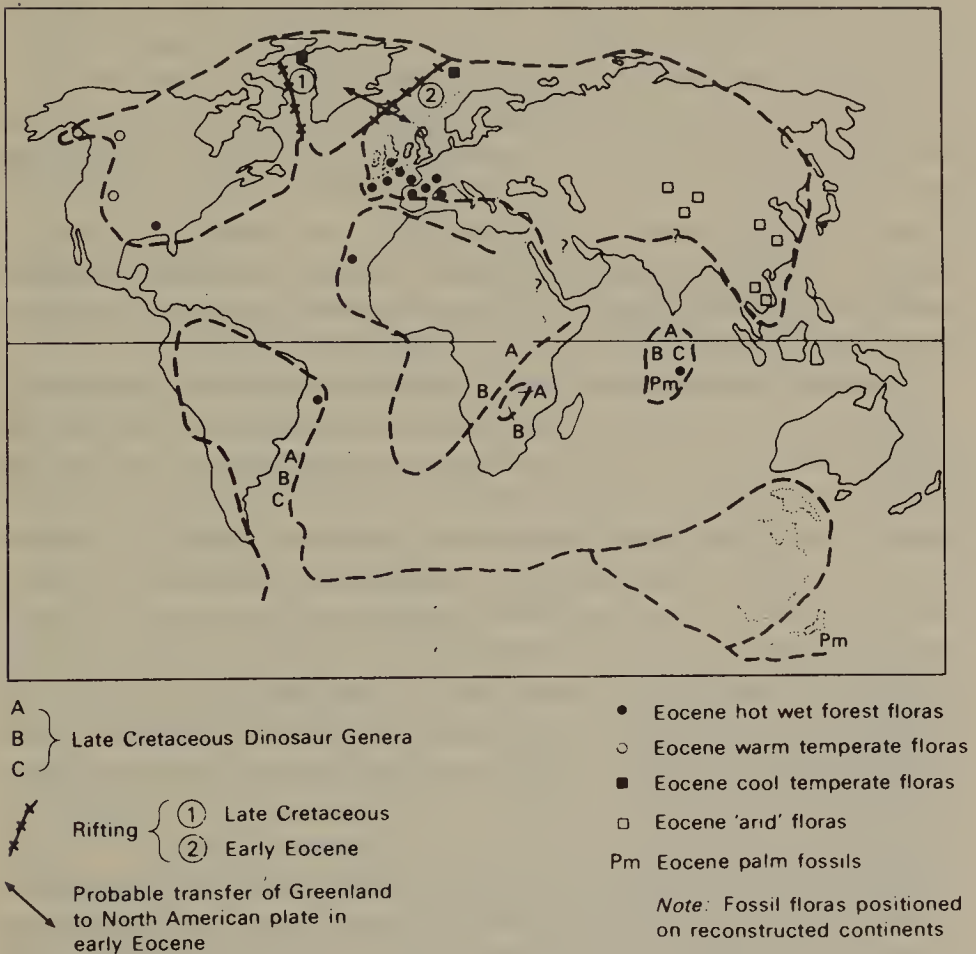
Figure 2.2 Possible position of continental masses at late Cretaceous to early Eocene transition (Palaeocene). Note the high latitudes reached by hot wet forest floras and the anomalous positions of the Cretaceous dinosaur genera and Eocene palm floras. (Compiled from data in Dietz and Holden (1970), Pitman and Talwani (1972), Keast (1971), Hallam (1972) and Takhtajan (1969).)

began to fragment. Africa/South America bean to rotate away from Antarctica and from each other in the late Cretaceous, as did India, Australia and New Zealand in the Eocene. Laurasia on the other hand seems not to have been closely connected from the Jurassic onwards, and oceanic gulfs of no great extent existed between the land masses of North America, Greenland/Western Europe and Asia. During the Eocene, the Asian land mass was joined by the East Asian Plate, and India had collided with it by Miocene times.

The significance of the nature of the break-up of Pangaea in the two hemispheres is profound for the distribution of the flowering plants particularly.

In the earliest times of angiosperm evolution, i.e. the Cretaceous period, the continental separation was not so advanced that migration was not possible. There is some evidence, for example, that angiosperm types may have migrated from western Gondwanaland to the Laurasian continent. Also, similarities in the Cretaceous pollen floras of Africa and eastern Brazil show that a tropical migration route was present. This involved a southern temperate route – followed by the *Proteaceae*, for example – via Antarctica to South America. This temperate route is well exemplified by the southern beech genus, *Nothofagus*, and late Cretaceous fossils are found in New Zealand, Antarctica, Australia and South America.

During the Tertiary period, the migration routes of Gondwanaland were severed both by increasing oceanic separation of the continents and by the deterioration of the climate of Antarctica. As Africa and India moved equatorwards across the climatic zones, most of the plants of southern affinities were lost from these regions. Only in the extreme Cape Province tip and in Malagasy (Madagascar) are the southern affinities preserved. New Zealand and the southern tip of South America, in contrast, preserve some of the character of the ancient temperate forests. Australia, passing through some 15° of latitude, collided with the East Asian Plate some 15 million years ago, the evidence of that collision being preserved in the zone of mingling of southern and northern plants and animals called 'Wallace's line'.

Unlike Gondwanaland, the division of Laurasia was never so extensive that migration was not possible for most of the Tertiary period, at least for temperate plants. Old and New World tropical floras, in contrast, were divided from each other by the earlier opening of the South Atlantic.

Although authorities differ in their interpretation, there is general agreement that, in the Palaeocene and Eocene epochs of the
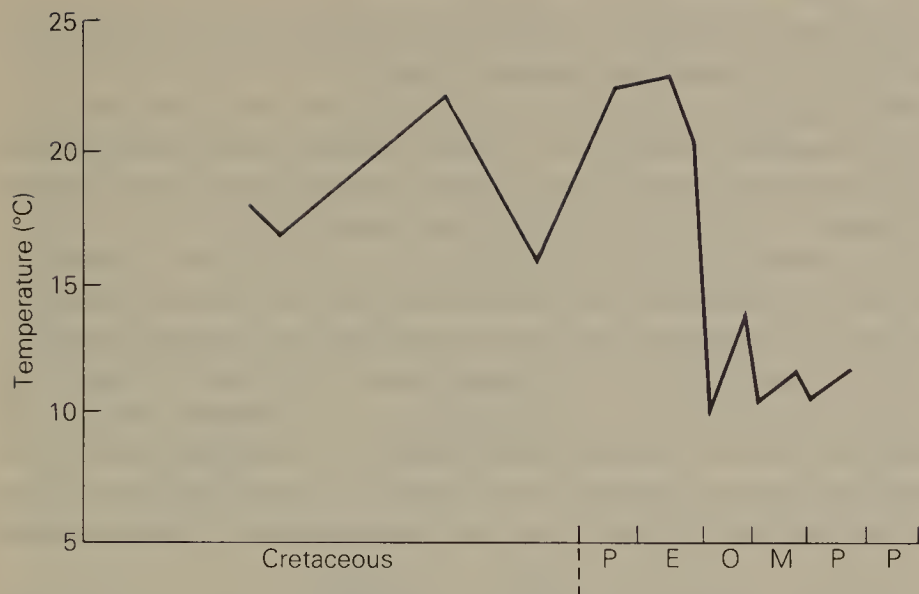
Figure 2.3 The course of palaeotemperature during the Cretaceous and Tertiary at palaeolatitude 45°N. (After Hallam (1983).)

Tertiary, the temperature was significantly higher than that of today, as can be seen from the temperature curve in Figure 2.3. These remarkable temperatures have been ascribed by some authors to a 'greenhouse effect' produced by increased atmospheric carbon dioxide derived from sea-floor hydrothermal activity, which added extra calcium to the marine ecosystem (Owens & Rea 1985). At the time of the peak temperatures in the Eocene, along the line of the Tethys Ocean at the southern edge of Laurasia to beyond 60°N, there existed a rich semi-tropical vegetation. A fossil flora from Kansas, for example, suggests a mean annual temperature of 25°C at the palaeolatitude. Another flora that has been particularly well studied, the Eocene London Clay (Chandler 1961–66), with over 400 species identified from 40 families, has many affinities with present-day tropical environments. This flora, with its prominent *Nipa* palm remains, has been compared to the present-day vegetation of the coasts of Malaya. However, some authors deny the essential tropical character of the London Clay flora and suggest that the fossils of tropical affinities were derived by long-distance river transport from more southern locations. The forests, unlike those of the present-day tropical lands, seem to have contained a mixture of tropical, semi-tropical and temperate types, with older taxa derived from the gymnosperm forests of the Mesozoic included as part of the floral mix. In contrast, in what is now central Asia, floras occurred with arid

affinities and some authors (Takhtajan 1969) suggest that this is the first sign of the 'dead heart' of the continent.

Although there is evidence that glaciation may have begun in Antarctica during the Eocene, the first sign of climatic deterioration in the rest of the world occurs at the end of the epoch in the Northern Hemisphere. This so-called 'terminal Eocene event' can be clearly seen in Figure 2.3. The dramatic fall in temperature across the Eocene/Oligocene boundary profoundly affected the vegetation of the hemisphere, although it was not until the Miocene that the full impact becomes obvious in the fossil record (Fig. 2.4). Through the Oligocene to the Miocene, tropical types are gradually reduced and replaced by a more temperate vegetation of mixed deciduous and evergreen angiosperms together with coniferous trees. This forest type, labelled the Arcto-Tertiary flora by Axelrod, seems to have persisted
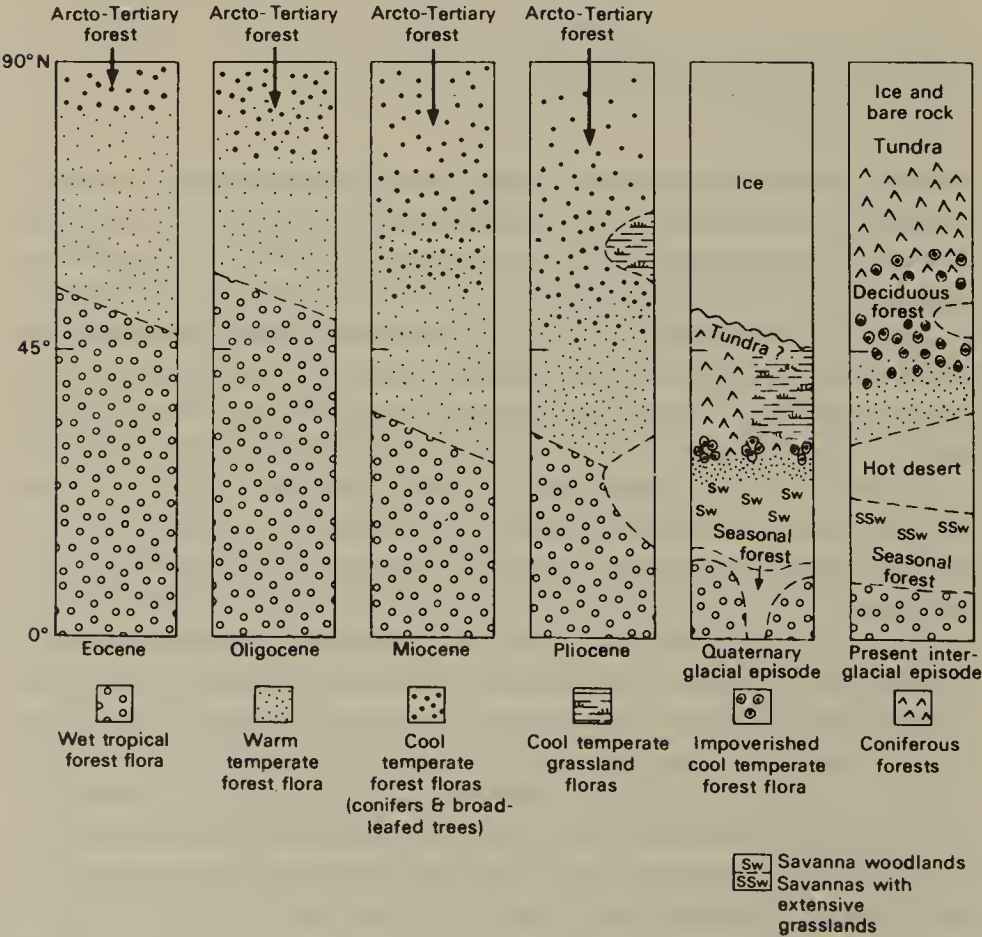
Figure 2.4 The course of vegetational change on the west coast of a hypothetical continent in the Northern Hemisphere during the Cenozoic. Note the evolution of marked latitudinal zonation of vegetation during the Quaternary.

through the Miocene and into the Pliocene (Fig. 2.4), with the first significant temperate grasslands appearing in the former period. Signs of inland aridity also occur in the Miocene record of floras from the southwestern areas of North America where an oak-chaparral vegetation is represented. This aridity is also present in the Pliocene floras of southern Europe. The destruction of the Arcto-Tertiary forests began with the further sudden deterioration of the climate to the true glacial conditions with the onset of the Pleistocene glaciations.

Although the general outline of continental drift and its effects on the distribution of taxa and vegetation is agreed, there is much discussion as to details. Continental drift has not solved several of the most knotty problems of plant geography. For example, Figure 2.2 shows that, in India, dinosaur genera occurred as they did also in other southern continents at a time when the position of that continent precluded migration. Moreover, Sahni (1984) has pointed out that there is very little of the phenomenon of endemism in the flora and fauna of the continent, and its original population has affinities with that of Madagascar during the Cretaceous–Palaeocene transition. Another particularly difficult problem is presented by the islands of New Zealand, which still remain a 'biogeographic riddle' (Keast 1971), especially in relation to the animal taxa. Apart from bats, New Zealand has no mammals and there is no record of such as fossils. Fossil dinosaurs are also unknown, as are turtles and frogs. The flightless birds, until recently the dominant land animals, seem to have been already flightless before New Zealand acquired them in the early Tertiary, although many marsupials already existed. Did one group walk there and the other not? If so, where was the land they crossed? The flora is equally strange. In the early Tertiary, New Zealand had a rich flora of palms, as did India, yet these seem to be largely absent at that time in Australia. Analysed by Hooker in 1860, the then flora showed 50% of species (mainly conifers) to be endemic, with 25% shared solely with Australia and 12% with South America only. Many plant geographers have argued that this flora indicates (a) long isolation for New Zealand and (b) close connections at some time between New Zealand, Australia, Antarctica and South America. Both Darwin and Wallace argued against this view and suggested that the disjunct distributions of southern plants were relics of once widespread populations that had become extinct elsewhere. Darlington (1965) argues that the Antarctic continent formed the connecting link and that migration routes existed until Miocene times at least. Yet New Zealand acquired neither dinosaurs nor mammals, and Australia no palms until much later. Moreover,

the evidence of early Tertiary glaciation in Antarctica is quite strong. So the 'riddle' remains.

Even where fossil remains seem least equivocal, there can still be doubts as to their interpretation. The London Basin Eocene flora mentioned above, for example, occurs in sediments from the Upper Palaeocene (54 million years ago) to Lower Oligocene times (38 million years ago). This has been described (see above) as tropical rainforest with coastal swamps and, as the fossils present a wealth of detail, for once there are few problems of identification. Apart from the strictures already mentioned above, there is a major strati-graphical problem. At the same levels as this supposedly richly forested, wet lowland, not 200 miles away in the Paris Basin are thick gypsum deposits indicating very arid conditions. Applying the princi-ple of uniformitarianism (the present is the key to past), the only part of the world today where such conditions occur is along the Trade Wind coast of Ecuador. Whether the peculiar conditions of the coast can be postulated for Upper Eocene Europe, on the other hand, is a moot point. A contemporary example of what could become a similar future anomaly in the geological record is provided by the discovery of tropical fruits and seeds on the coasts of north-west Europe (Nelson 1978). This discovery illustrates the care that must be taken in interpreting marine records of terrestrial vegetation.

The examples above are admittedly extreme cases of some of the outstanding anomalies of plant geography but they demonstrate the pitfalls within the subject. As Schuster (1972) has pointed out, 'phytogeographic theory is particularly subject to distortion that served (a) to reinforce a previously accepted viewpoint, and (b) omits all the potentially embarrassing bits of evidence'.

2.5   Quaternary climatic change

Although there is evidence of glaciation in Antarctica as early as the Eocene and in midlatitude Southern Hemisphere mountains in the Miocene period (Mercher 1983), the first widespread glaciation occurred in the Southern Hemisphere in Pliocene times (3.2 million years ago (my BP). This was followed by a non-glacial interval but recurred with the onset of Pleistocene times when ice became widespread in the Northern Hemisphere as well. (Figure 2.5 shows the preglacial vegetation pattern for Western Europe.) From then on, glaciation appears to have been synchronous in both hemis-pheres, Antarctic ice volumes being controlled by the Northern

----- Shorelines
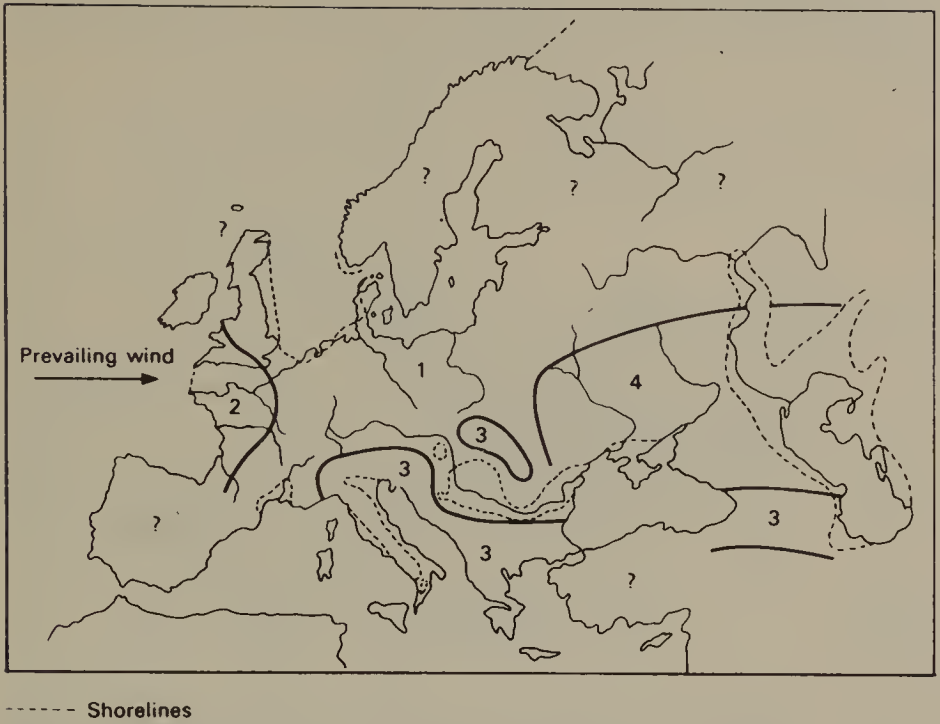
Figure 2.5 The vegetation pattern of Europe at the end of the Pliocene. (1) Cool temperate Arcto-Tertiary forest (conifers and deciduous trees as mixed stands). (2) Oceanic forest of pine, *Sequoia* and other conifers with heather undergrowth. (3) Mixed warm temperate forest with warmth- and moisture-loving trees. (4) Forest with prominent grasslands. (After Frenzel (1968) and Wijmstra and Van der Hammen (1971).)

Hemisphere ice sheets as these formed and disintegrated. The repeated episodes of glaciation during the Pleistocene had profound effects on all the world's floras (not only those in the higher latitudes), extinguishing species, stimulating the evolution of adaptations in others, and disrupting or modifying the geographical range of the majority. As Good (1974) has pointed out, the geography of land plants today is the geography of a flora lately subjected to a major disaster.

The most significant effects of glaciation were those felt in western Eurasia, where the richly varied forests – the so-called Arcto-Tertiary forests – which had clothed the lands for so long in the Upper Tertiary, were utterly destroyed. The broad-leaved forests were reduced to a few genera – oaks, limes, hornbeams, beeches, elms, etc. – surviving in the Balkans and Apennines (Fig. 2.6). In North America and eastern Asia, continental migration routes to the south allowed the Pliocene types to retreat much more easily before the onslaught of cold conditions, and the warmth-loving trees – the

Mixed forests
mainly conifers

Steppe with groves
of hardy trees

Steppe grassland

Tundra

Ice cap and
mountain glaciers

D   Probable area
without plant life
('arctic' desert)

Shoreline

R   Main refugia of
deciduous broad-
leaf species
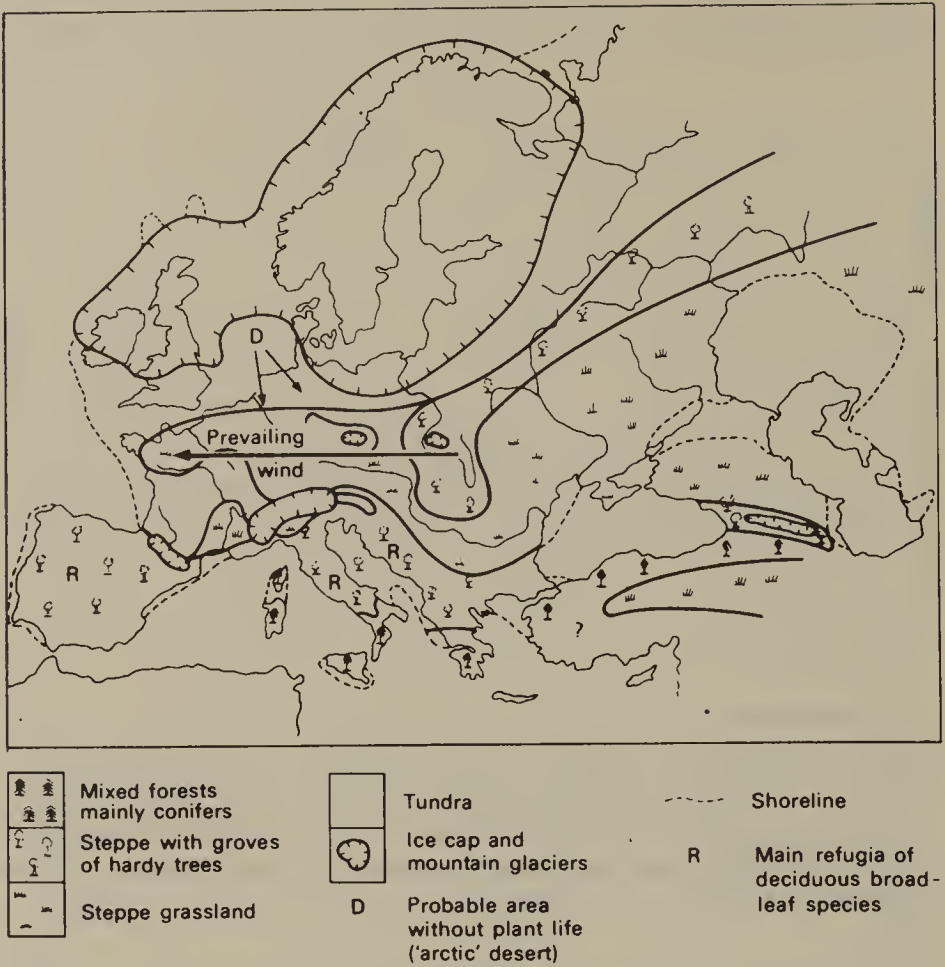
Figure 2.6 Vegetational pattern of Europe during the last glaciation. (After Frenzel
(1968) and Wijmstra and Van der Hammen (1971).)

walnuts, pawpaws, sweetgums, hickories, persimmons and tulip trees
– were able to shelter in the southern Appalachians and south-east
China.

In the highest latitudes of all in the Northern Hemisphere, the
tundra as a vegetation type seems to have been destroyed and to have
re-evolved several times during the Quaternary (Frenzel 1968).

Tropical oceanic cores provide interesting evidence that tropical
areas in Northern and Southern Hemispheres during the Quaternary
had significantly different climatic regimes during glacial and intergla-
cial episodes. For example, Atlantic cores from the ocean adjacent to
central Africa show that during glacial episodes tropical central
Africa north of the Equator became arid, whereas the Southern
Hemisphere central African tropics (Angola) became more humid.
This has been ascribed to the southwards displacement of the

intertropical front following intensified oceanic circulation in the Northern Hemisphere. The authors who present this evidence (Jaensen *et al.* 1986) suggest, therefore, that glacial/interglacial conditions are not compatible in the tropical lands of the two hemispheres.

The details of the early stages of the Pleistocene are not well known, and differing terminology is applied in North America and Western Europe (see Table 2.1).

Note that the status of the divisions even of the later Pleistocene is not yet completely certain. The Ipswichian, for example, has been re-examined and evidence has been produced that it may have encompassed considerable climatic variation. Two distinct warm episodes have been identified from cave faunal deposits, for example (Moore 1986). Also, the Anglian glaciation may contain an interglacial between 350000 and 300000 BP as evidenced from ancient flint working in southern England.

Based on terrestrial deposits, the pattern of recolonization in Britain can be discerned from the Pastonian onwards, and this pattern seems to have been followed in broad terms in the succeeding interglacials in Northern Europe. Pioneer birch was followed by pine with light-demanding herbs common in the open woodlands. As soils were enriched by these pioneer species, they were colonized by hazel, oak and ash to produce a climax forest. When conditions deteriorated once more, minerals began to leach from the soils and climax trees

Table 2.1 Terminology of early Pleistocene.

Great Britain	Northern Europe	Central Europe	North America	Years BP (×1000)
Flandrian	Holocene *Flandrian*		Holocene	10
Devensian	Weichselian	Wurm	Wisconsinan	80
*Ipswichian**	*Eemian*		*Sangamon*	100
Wolstonian (Gipping)	Saalian	Riss	Illinoian	200
Hoxnian	*Holsteinian*		*Yarmouthian*	250
Anglian*	Elsterian	Mindel	Kansan	350
Cromerian	*Cromerian*		*Aftonian*	400
Beestonian	Menapian	Günz	Nebraskan	
Pastonian				
Baventian	Early Pleistocene (Villafranchian)			
Antian				
Thurnian	Tegelen			
Ludhamian				
Waltonian				3000
Pliocene (Reuverian)				

*Terminology from West (1977).

were eliminated to be replaced by birch, pine and heath and finally
arctic tundra. In the earlier interglacials, some Pliocene species were
present such as hickory (*Carya*), but the most severe glacial epoch,
the Anglian, eliminated these from Europe altogether. A variation of
the pattern is thought to have occurred in the Ipswichian (Sangamon)
interglacial, where plants spread beyond their current polewards
limits in both Eurasia and North America, suggesting a warmer
climate than at present. Figure 2.7 gives an indication of the Earth's
vegetational pattern during the last glacial episode, but the rather
broad category of 'forest and well vegetated areas' illustrates one of
the major problems of reconstructing the climate and vegetation in
Quaternary studies. Reconstructions rely heavily on the interpreta-
tion of the fossil pollen record (palynology). While pollen is particu-
larly suitable for this purpose in some respects, in that it is the most
abundant fossil material, is resistant to decay and has a well known
taxonomy, it has drawbacks. In particular, it is likely to be much
travelled. For example, *Ambrosia* pollen is found in British sites in
the Isle of Skye (Birks 1973), when it could only be derived from
across the Atlantic. In North American sites in central and eastern
USA, late Wisconsinan deposits consistently contain pollen from
warmth-loving trees, which were certainly not present within the
region.

Figure 2.7 The world land, sea and vegetation pattern 18000 BP. (After Climap
1976).) Dashed lines enclose areas where sea surface August temperatures were at
least 4°C below those of today.
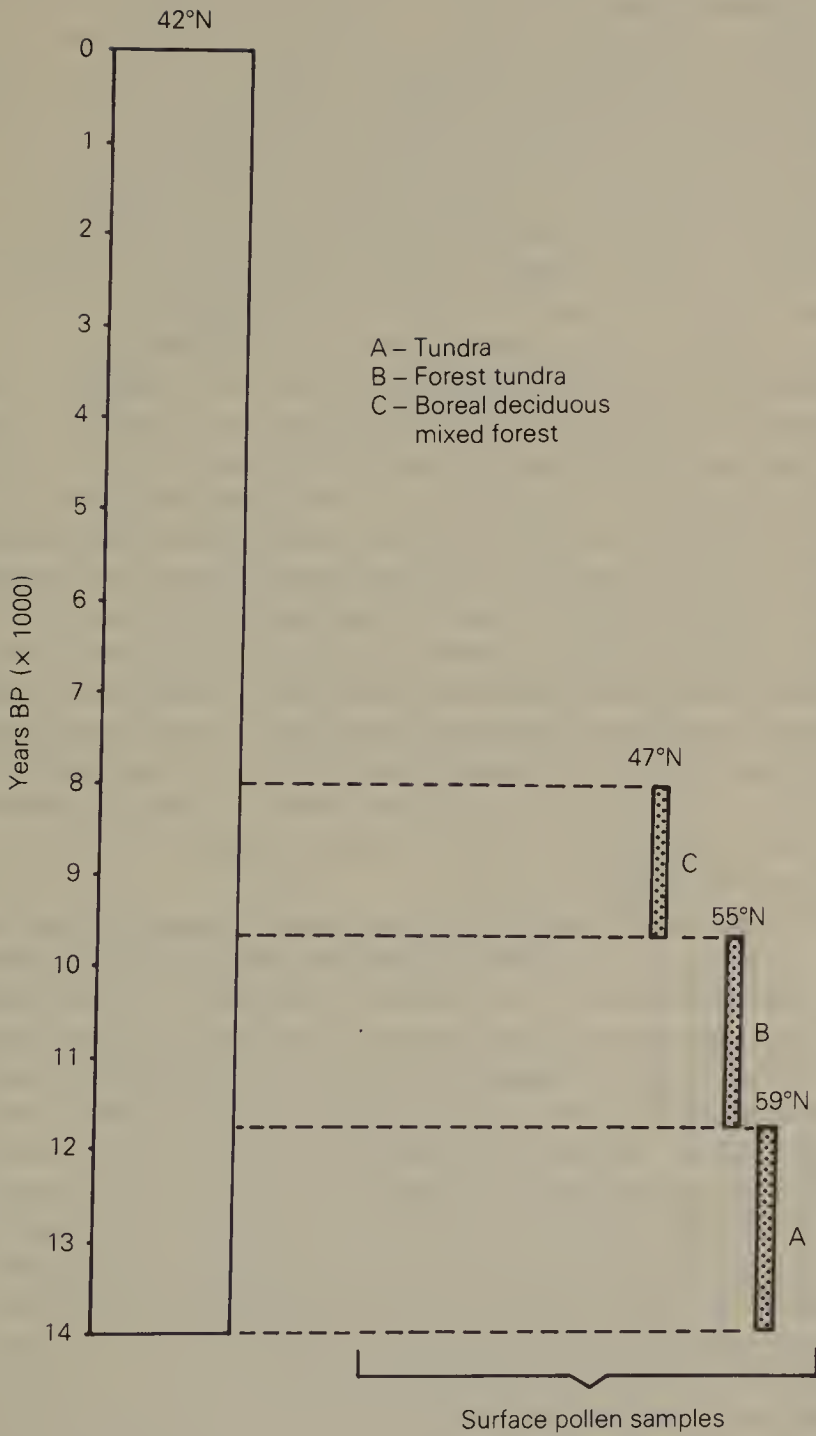
Figure 2.8 Comparison of surface pollen sample (A,B,C,) with fossil pollen samples from cores in New England.

In spite of these and other difficulties, there is general agreement that modern techniques of pollen analysis and interpretation are sufficiently sophisticated to give a reasonably coherent picture of the later stages of Quaternary vegetational evolution (Bernabo & Webb 1977, Birks & Birks 1980) and also the contemporary relationships of pollen deposits and vegetation (Davis & Webb 1975). Maps have been produced, for example, tracing vegetational changes for Europe and eastern North America from approximately 40 000 BP (Frenzel 1968, Davis 1976, Huntley & Birks 1983) and new details are constantly added. (Figure 2.8 compares contemporary surface pollen with fossil pollen in cores from eastern North America.)

Unlike the European section of the Northern Hemisphere, where it is generally accepted that the longitudinal barrier of the southern mountains and Mediterranean prevented migration to safe refugia during glaciation, in North America and east Asia many of the warmth-loving taxa were able to migrate southwards with the shifting climatic belts. About 15 000 BP unglaciated areas in north-west Europe carried an open, tundra vegetation (the 'Lower Dryas' deposits) with fossil floras characterized by *Dryas octopetala* (mountain avens). Between 12 000 and 10 500 BP the climate ameliorated sufficiently to allow an open park woodland to become established (the Allerød phase). The vegetation of this interstadial disappeared from most of the area in the succeeding return to periglacial conditions during the brief Upper Dryas, which marked the end of the Devensian glaciation.

In the Southern Hemisphere, deglaciation seems to have begun earlier than in the Northern Hemisphere (Mercher 1983) around 14 000–12 500 BP, with a possible later readvance in New Zealand. The North American continent, with its huge ice sheets, had a much slower deglaciation, although the western side of the continent was soon colonized from about 13 000 BP, as trees had never retreated very far from the ice edge. In this area *Pinus*, *Tsuga*, *Picea*, *Abies* and *Pseudotsuga* species spread northwards very soon after the cordilleran ice retreated (Barnosky 1985). Unglaciated inland areas in the western part of the continent display an interesting time lag between the loss of Wisconsinan plants between 18 000 and 5000 BP and the influx of colonizing Holocene taxa. This tendency for plants to remain *in situ*, although the original conditions to which they were adapted have changed, has been termed 'vegetational inertia' (Cole 1985). The reasons why plants can survive in unsuitable climatic environments depend on the particular circumstances of their location. A much studied example is that of the vegetation of Upper Teesdale

in County Durham, England. Here a late Devensian and early Holocene flora that includes *Betula nana* (dwarf birch), *Dryas octopetala*, *Gentiana verna* (spring gentian), *Juniperus* (juniper) and *Thalictrum alpinum* (alpine meadow rue) has survived in a refugia created by a peculiar combination of geolgical and climatic conditions. It was the fight, carried ultimately unsuccessfully to the House of Lords, to save this unique flora from reservoir construction in the 1960s which first fully alerted the British botanical community to the threat that modern development can present even to sites of the highest scientific quality.

On the eastern side of North America, deglaciation was more tardy than in Eurasia. The ice cap still extended to the Great Lakes–St Lawrence basin at the time of the onset of postglacial climates in Western Europe (9500 BP). As the climate ameliorated, the forest belts moved northwards but were checked by the expansion of dry grasslands to the east (the so-called prairie peninsula (Fig. 2.9)), reaching a maximum around 7000 BP. There is some evidence that later 'xerothermic periods' around 4000 BP and from 1000 to 700 BP extended grassland to the Atlantic coast and far into the Great Lakes region, leaving forest relics. This may have resulted from extensive firing by lightning and aboriginal burning practices. At the time of the climatic optimum (7500 to 5000 BP), forests of spruce in the centre of the continent seem to have extended, together with hardwood forests, 2–3° of latitude further north than at present.

Deglaciation was marked in tropical Arabia, Africa and South America by changes in rainfall regime. The pluvial conditions of late Pleistocene began to wane from 18000 BP to low rainfall levels around 14000 to 12000 BP. Rainfall then increased once more, producing extensive lakes, as in West Africa, which dried out again around 5000 BP (Kerr 1984). Evidence also exists that the atmospheric **lapse rate**, at present around 0.6°C/100m, during the Pleistocene was around 0.8°C/100m (Fig. 2.10). In the tropical parts of New Guinea, for example, montane forest limits of 2200m altitude during the Pleistocene extend to 3500m at present (Whitmore *et al.* 1982). In north-west Europe the course of postglacial climatic changes and the associated vegetational palaeoecology has been intensively studied over this century to give today a well agreed history. The pioneer of this study in Britain, H. Godwin, argued that the zones identifiable in the pollen stratigraphic record reflected climatic phases to which the vegetation had responded (Godwin 1975). Later work may have refined Godwin's original sequence, for example by more precise dating as the techniques of radiocarbon analysis and calibra-
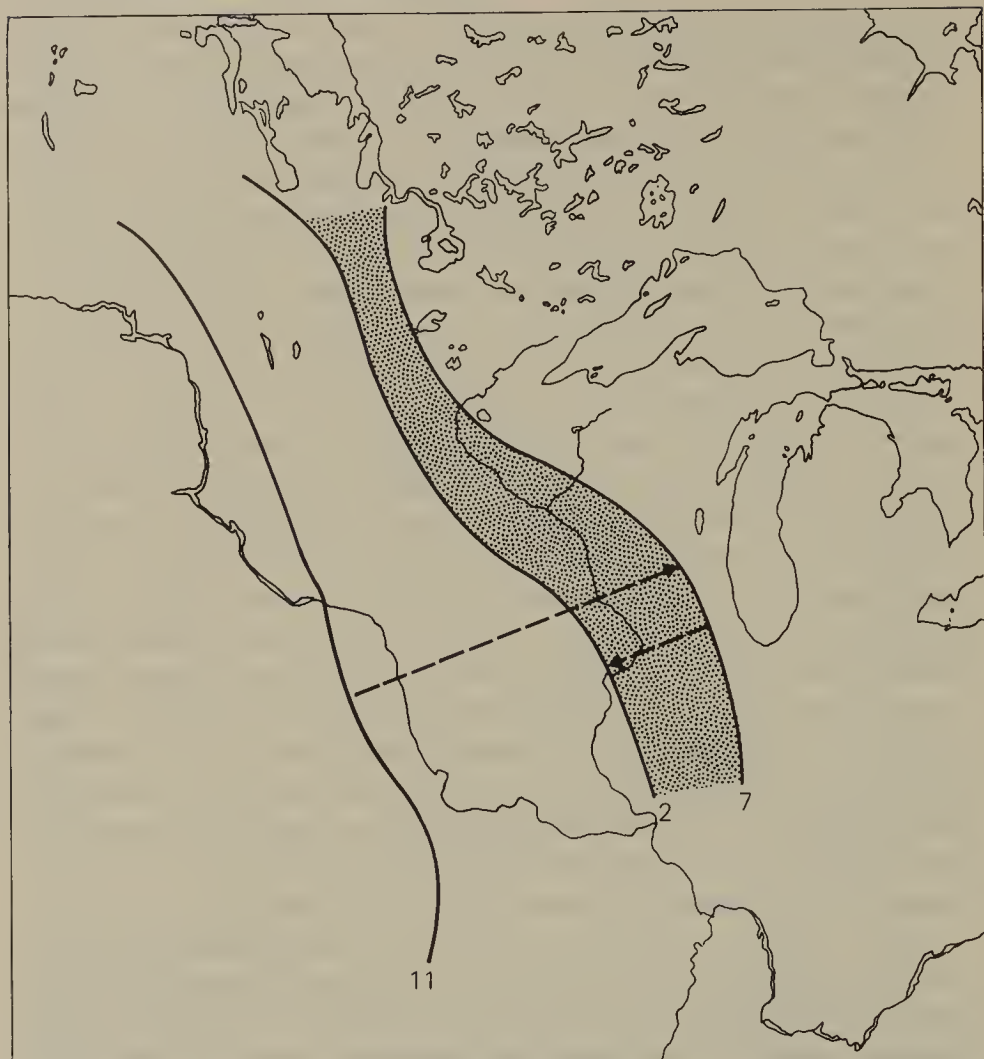
Figure 2.9   The advance and retreat of the prairie peninsula. Figures are thousands of years BP. (After Bernabo and Webb (1977).)

tion have improved, but the general picture is now well established. Table 2.2 shows the dating and nature of the sequence.

The climatic optimum within this sequence, the Atlantic phase (7500–5000 BP) was reflected in the widespread abundance of oak and elm, with the addition to the British flora of *Tilia* (lime), one of the most sensitive of cool temperate forest plants to cold conditions. In Scandinavia, *Hedera helix* (ivy), also sensitive to cold, was at a maximum. The mild conditions were reflected also in the extension of the tree lines to levels beyond those of the present day. In Britain (apart from the Scottish Highlands and Islands), mixed oak forests reached 750 m (2450 ft). However, the period was not only mild but
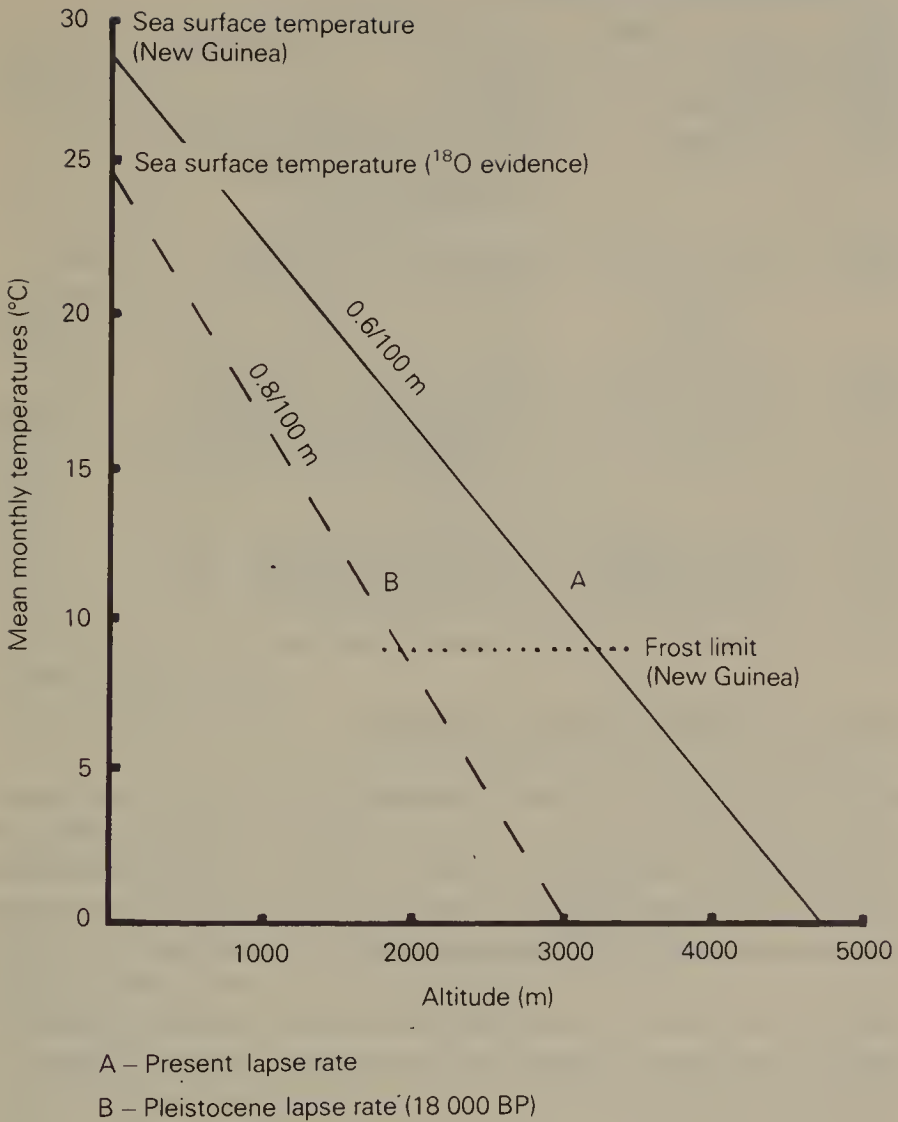
Figure 2.10 Pleistocene and contemporary lapse rates. (After Flenley (1979).)

seems to have been very wet, a condition reflected in the abundance of *Alnus* (alder) pollen in the record. The intensity of the rainfall regime encouraged the growth of peat on areas of poor drainage and the raised bogs and blanket peats characteristic of much of upland Britain began to develop at this time.

This mild phase ended with the onset of the Sub-Boreal and was marked in the pollen record by a sharp decline in elm pollen and an increase of pollen from plants of open environments such as *Rubex* spp. (docks) and *Stellaria media* (chickweed). Thorny plants resistant to grazing, such as *Ulex europaeus* (gorse) and *Crataegus monogyna* (hawthorn), also became important at this time. These changes have

Table 2.2　Postglacial climate and vegetational change in Britain.[*]

Years BP	Climate	Vegetation	Pollen zones
2500	Sub-Atlantic	Increase in birch; elm pollen very low, also lime; beech and hornbeam increase	VII
5000	Sub-Boreal: drier, somewhat continental	slight decrease in alder, lime, possibly oak; slight increase in birch	VIIb 'Elm decline'
7500	Atlantic: moist, warm oceanic	mixed oak forest; dominant oak with alder, elm and lime; hazel abundant but pine and birch very reduced	VIIa Flandrian II
9500	Boreal: continental, increasingly warm	decreasing pine; abundant hazel; increasing elm and oak	VI
10 000	Pre-Boreal: cold	dominant birch with pine	IV Flandrian I

[*] Data from Pennington (1974) and West (1977).

been linked (a) to an increase of continentality, (b) to an immigration of people of Neolithic culture creating cleared land for farming, and utilizing elm as cattle fodder, and (c) to the ravages, in the case of elm, of the elm bark beetle (Girling & Grieg 1985). Good evidence has been presented for all three as affecting the vegetation of Britain at this time. Certainly, the clearance of land, especially the lighter soils, was very effective, and by the ensuing Bronze Age (4500 BP) much of the light soil uplands of eastern and southern Britain had become grazing land.

2.6　Human influence on postglacial vegetational change

The pioneers of pollen stratigraphy assumed that changes in the pollen record usually meant changes in the climate, but over the years, in Western Europe at least, this theory has been hard to support. For example, in Britain, Godwin put the Atlantic/Sub-Boreal boundary (originally identified in Scandinavia) at a level where elm pollen practically disappears from the record. Diligent searching for other evidence of climatic change at this level has yielded very little. What explains the spectacular decline of one genus simultaneously over wide areas of Europe? With its present ravages,

it might be suggested that Dutch elm disease or something similar could have been the cause, but there is another clue. Both anthropologists and archaeologists have pointed out that the foddering of animals on leaves of the elm and other plants is still practised in parts of Europe and may have been widespread amongst the herdsmen of **Neolithic** times. Certainly, hoards of elm leaves have been found in excavated sites. Perhaps the elm might have been cut so extensively – the easily accessible younger trees especially – that it almost became a rare plant (Pennington 1974).

It might be thought that the low human population could have had little effect on thick temperate forests, but an experiment carried out in Denmark illustrates the effectiveness that even simple technology can have. In that country, variations of tree pollen above the level of the elm decline are associated with episodes of clearing, burning and cultivation called 'Landnam' clearances. Using stone axes from the national museum, newly hafted in the manner of the Neolithic times, some $600\,m^2$ of West Jutland forest were cleared by two men in just 4 h (Pennington 1974).

In some peat deposits, two distinct periods of decline of elm pollen can be detected. The first is dated between 5000 and 5400 BP, the second from 4300 to 4250 BP approximately. As to the precise causes for these declines, as well as the activities of people of Neolithic culture noted above, there is some evidence in some sites of the presence of the elm bark beetle (Girling & Grieg 1985) and some evidence for additional factors deriving from climatic and erosional changes (Hiron & Edwards 1986).

In North America, the equivalent to Atlantic conditions in northwest Europe is the so-called Hypsithermal. Various dates for its commencement are given spanning the period from 10000 BP to between 7000 and 5000 BP. The termination dates also vary depending on the region, for example 6600–6000 BP in British Columbia, 4800 BP in the Okanagen Valley, 3300–3000 BP in eastern Washington and in some eastern areas as late as 1500 BP (Dunwiddie 1986).

It has long been noted that the flora of the British Isles is much impoverished when compared to near continental areas. This is due to the long separation from the continent resulting from the successive rise of sea levels as the great ice sheets melted. Three marine transgressions (West 1970) have been noted (Flandrian I, II and III): the first, at the end of the Boreal, divided Ireland from Britain, and the second, during the Atlantic, flooded the North Sea, preventing migration from the east. By the end of Atlantic times, the opening of the English Channel completed Britain's isolation.

The onset of the Sub-Atlantic period saw a world-wide deterioration of climate, not synchronous everywhere. The deterioration culminated in the so-called 'Little Ice Age', which lasted from the 17th century to the end of the 19th century. The adjustment of plant communities to fluctuations of climate in the Sub-Atlantic is very difficult to extricate from the overriding effects of the activities of humankind in most parts of the world. The effects of fire, clearance for agriculture and forestry, and the needs for domestic fuel and grazing land have affected so much of the world's vegetation that relatively few areas of temperate or tropical lands remain untouched. So far has this process gone in some parts of the world that, to the words of Good above, we must add that, not only has the world's flora lately undergone the disaster of the Pleistocene, but also that it is undergoing an equal if not greater disaster at the hands of human beings.

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3

Ecology, biogeography
and energy variations

3.1 The principles of ecology

To answer two questions that concern the ecologist and biogeographer, 'Where do species live?' and 'Why there?', geological history can only take us so far along the road. We need also to know the way plants live now and what in their present environments encourages their growth or limits their spread. It is to the science of ecology that we must look for insights, techniques and principles to guide our understanding in this task.

Ecology has recently caught the public attention in no uncertain way and has come to the fore in the last three decades as much as a result of a change in its own methods as of a desire on the part of the public to learn some scientific natural history.

The development of the dynamic and rapidly growing study of today can be dated almost exactly to the publication in 1942 of a paper by a brilliant young American biologist, F. E. Lindeman – later a tragic victim of World War II – concerning the quantification of the relations between organism and environment, especially the exchanges that take place in energy and materials. From that time, the subject of ecology has been transformed, by the application of measurement and mathematics, into a considerably more precise scientific study. With the publication of each paper since that time on matter and energy exchanges, it has become more and more apparent that organism and environment are so inextricably intertwined that to consider them separately is almost impossible. Only a concept of ecology that places the unity of living and non-living matter at its heart can do full justice to natural phenomena on this planet.

This insight is one of the most important contributions science has made to the understanding of our world so far this century, and its echoes reverberate into fields far from the ecologist's laboratory.

The key to modern ecology lies in the concept of the **ecosystem**, a concept introduced by the great British ecologist, Sir Arthur Tansley, in 1935 when he designated them as the 'units of nature'. This concept implies that (a) all plant and animal communities, without exception, together with the non-living world they inhabit and partially fashion, form unified systems, and (b) these systems are maintained by the production and flow of energy within them and the circulation of materials between the living and non-living matter that composes them, i.e. they are wholly unified (**holocoenotic**). Ecosystems can be as small as a living-room fish tank or as large as an equatorial forest, because the principles that govern their operation remain the same whatever the scale. It is implicit in this concept that there can be no duality of 'living things' on the one hand and 'environment' on the other. Plants and animals are as much environment as the air they breathe or the soil they live in or the food they eat; the duality is an illusion.

It must always be remembered, however, that each plant and animal is genetically distinct and each must work out its own relationship with whatever circumstances prevail in any particular ecosystem. If its genetics do not 'fit', it will not become established; if they do, then under the right circumstances it may well become established.

The 'right circumstances' depend on the availability of a suitable ecological **niche** within the ecosystem. The concept of niche is central to modern ecology and may be thought of as 'the way of life' of the species in the environment in which it is established. To enable a species to establish a suitable way of life, i.e. to occupy a suitable niche, its genetics must allow it to 'mesh' with all the circumstances that define the particular ecosystem.

The rules that govern the number of species within an ecosystem are complex and probably better understood in the case of animals than plants (see Ch. 7). However, one model that has been applied to both animals and plants with success was put forward in 1967. This is the celebrated 'theory of island biogeography' of MacArthur and Wilson (1967), mentioned in Chapter 1, which postulated that, for islands, the equilibrium point for species number rested on the intersection of two curves, the rate of extinction and the rate of immigration. The slopes of these two curves would depend especially on the size of the island and the distance from the sources of colonization.

As a corollary of their theory, they also suggested that the pressure of colonization would tend to select species into two major groups,

r-selected and *K*-selected types. The former would represent species that are successful in unsaturated environments (pioneer species, early successional types); the latter would represent species successful in saturated environments (late colonizers, climax vegetation types). Since its publication, the concept has been widely applied beyond its original 'island' framework, as it was realized that nature reserves, parks, pit heaps, cut-over mature forest, fire-cleared areas, etc., could all be seen in some circumstances as analogous to islands. Also, the utility of the concept of *r* and *K* selection has been widely recognized beyond the original model. The reader will find frequent reference to this in ecology and biogeography as well as in subsequent sections of this book.

Following Odum (1963), the circumstances that shape the character of ecosystems can be listed as:

(a) energy, its production and flow;
(b) materials – the inorganic chemicals (**nutrients**) out of which living matter is formed;
(c) conditions – the prevailing circumstances of place in which the ecosystem operates; and
(d) **community** – the plants and animals and their interactions that compose the living part of the ecosystem

In addition, the activities of human beings play a greater or lesser role in most ecosystems, although in some respects (e.g. radioactive pollutants) the effects are virtually universal. A practical ecologist would worry very little about the niceties of whether a particular factor represented 'condition' or 'community' or 'material'. The categories are used only as a broad organizational device through which the component parts of the ecosystem can be isolated for examination. One thing that can be said about these determinants of ecosystem operation is that each has a very definite geographical aspect at almost every scale from that of the Earth's **biosphere** (i.e. the atmosphere, oceans and rocks containing living material) to the strictly local.

Although each ecosystem is unique to some extent, broad generalizations may be possible about some of them, as certain factors such as climate or mineral supply may dominate the working of the system and may therefore have acted as a strong selective force in the evolution of the organisms concerned. Thus, similar adaptations may appear in similar circumstances. It is for this reason that broadly similar categories of vegetation – forests, grasslands, desert scrub,

etc. – have been fashioned by convergent evolution from the very different groups of plant types shown in Figure 1.2

3.2   Ecosystems and energy

Apart from certain micro-organisms (termed *chemautotrophs*) – for example, chemosynthetic bacteria – which obtain their energy via the oxidation or reduction of simple inorganic chemicals, the foundation of life is the Sun's radiant energy. This is received by plants in three distinct forms, thus:

0·3		0·4	0·5		1·0	2·0	3·0	10·0	Wavelength (μm)
ULTRA-VIOLET			VISIBLE		INFRA-RED				
Absorbed but functions obscure			Photosynthetic waveband		Important in growth regulation				
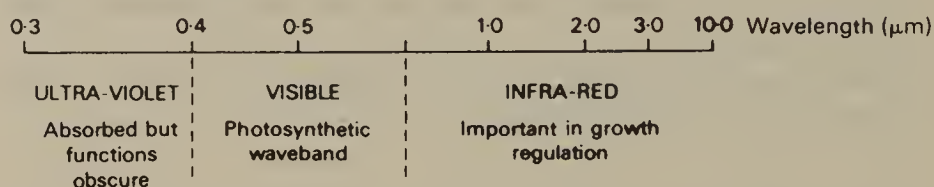
Plants absorb strongly throughout this range – apart from a very narrow band in the infra-red – but the destination of much of this **radiation** (especially in the ultra-violet) is still not completely known. However, it has been shown that near ultra-violet radiation has important effects on arctic–alpine species (Caldwell *et al.* 1982, Sissons & Caldwell 1975, Klein, 1978).

The quanta (or 'energy packets') of which radiant energy consists have insufficient energy in the visible light wavebands to bring about by themselves the combination of carbon dioxide and water to form carbohydrates. Instead the energy absorbed by chlorophyll – especially in the blue and red frequences – and other pigments is transferred to electrons to produce strong oxidizing and reducing agents. It is these which help to build the energy bonds in the primary products of photosynthesis, i.e. sugars and a compound called adenosine triphosphate (ATP). The latter acts as an energy donor to a vast number of metabolic reactions.

The amount of food created by green plants in an ecosystem is called its *gross production* and this is used by the plants themselves in their own respiration to sustain their life, but in all ecosystems they produce a surplus which is called the net **primary production**. It is this surplus that is used for growth and by the herbivorous animals and the rest of the food chain as shown in Figure 3.1

At every stage in the food chain from green plant to herbivore to carnivore, there is a loss of the total energy passing along the chain of the order of nine-tenths (this is the so-called '10% rule'). Agricultural ecosystems minimize the loss from stage to stage, and as much as
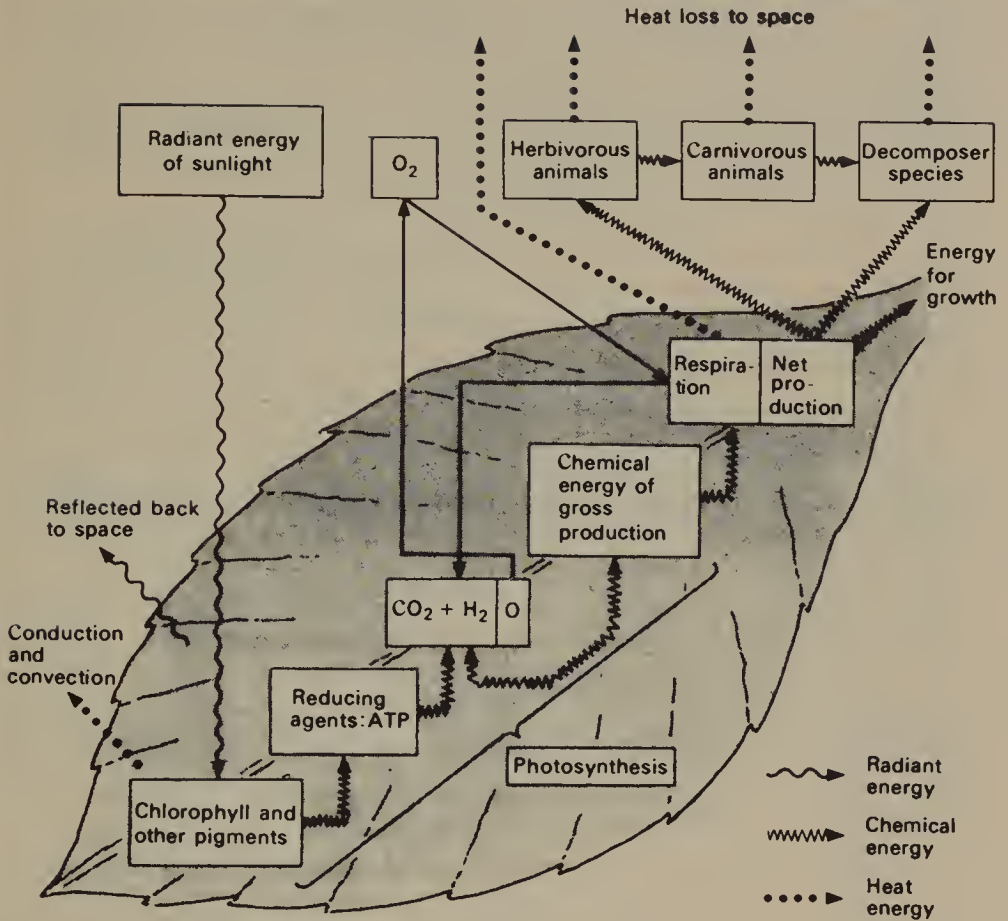
Figure 3.1 Energy flow in an ecosystem. Note that the units of measurement of production are normally given as the dry weights of organic matter per unit area of ground per unit of time. These may be tonne $ha^{-1} y^{-1}$, $kg ha^{-1} y^{-1}$, or $g m^{-2} y^{-1}$, and in some continental literature the *centner* (50 kg) may be used.

25% of the total energy available as food may pass from crops to humans, their animals and various pests (Figs 3.2 & 3.3).

Only a small fraction of the energy available to green plants is actually converted to food. Figures vary from one vegetation type to another. At the greatest efficiency, for example in rapidly growing barley, as much as 14% of the total incident light has been observed to convert to food for short periods. However, on a year-round basis, the figures are much lower. Figures for natural vegetation are usually much lower than these; perhaps less than 0.5% only of the total annual incident radiation is converted to food (Leach 1975). Although this figure may seem low, in fact natural vegetation overall traps more of the incident radiation annually than do crops. Wholesale removal of the latter in single-crop economies leaves bare
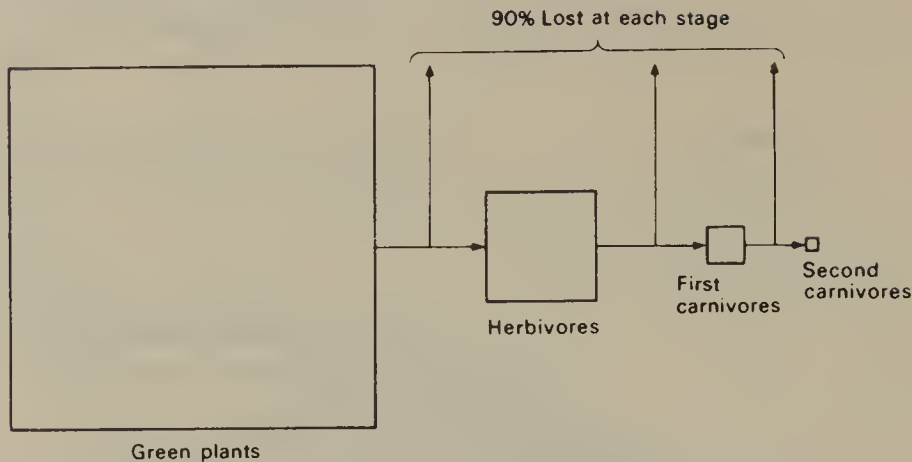
Figure 3.2   The relative amounts of energy passing along the food chain in a natural ecosystem.
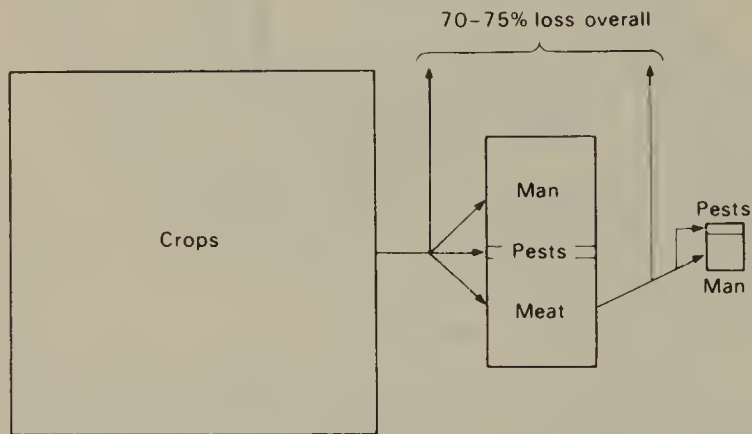
Figure 3.3   The relative amounts of energy passing along the food chain of an agricultural ecosystem.

ground unproductive for long periods. Only where multiple cropping of the land with irrigation is used do crop conversion figures match the energy trapped by natural vegetation on a year-round basis.

There is some evidence that photosynthetic production can vary under the influence of internal hormonal regulation. Fujii and Kennedy (1980) demonstrated that, in apple trees, higher photosynthetic rates occur in flowering and fruiting trees than in non-flowering and non-fruiting trees, and they suggested that it is induced by hormonal production by the flowering parts. Other internal, physiological changes also influence net primary-production (NPP). Vitousek (1982), for example, found that plants in nutrient-poor soils are able to use nutrients more efficiently in NPP and that stands became more efficient as they aged as nutrients were relocated

internally within the plant. In the pines studied, the process of relocation may result in needle loss and so decreased productivity (Gholz *et al.* 1985). (For a review of light and photosynthesis see Osborne and Raven (1986) and for a brief account of photosynthetic pathways and their biogeographical implications see Sec. 13.1).

3.3 Variations of production

By careful estimation of the solar radiation input to the Earth's surface and assuming that plants are fully using the fraction of radiation needed for photosynthesis, it is possible to obtain estimates of the geographical variation of potential net photosynthesis in regions where plant growth is not limited by lack of water or permanently low temperatures. Figure 3.4 indicates the latitudinal variation of these estimates. (Note the surprisingly high estimates for the summer months produced by increasing day length in higher latitudes.) Publication of the results of the International Biological Programme's efforts to measure actual net primary production in all the world's major ecosystems (Lieth & Whittaker 1975) shows quite clearly that none of them even nearly approaches the theoretical limits. Only in certain tropical agricultural systems – sugar cane
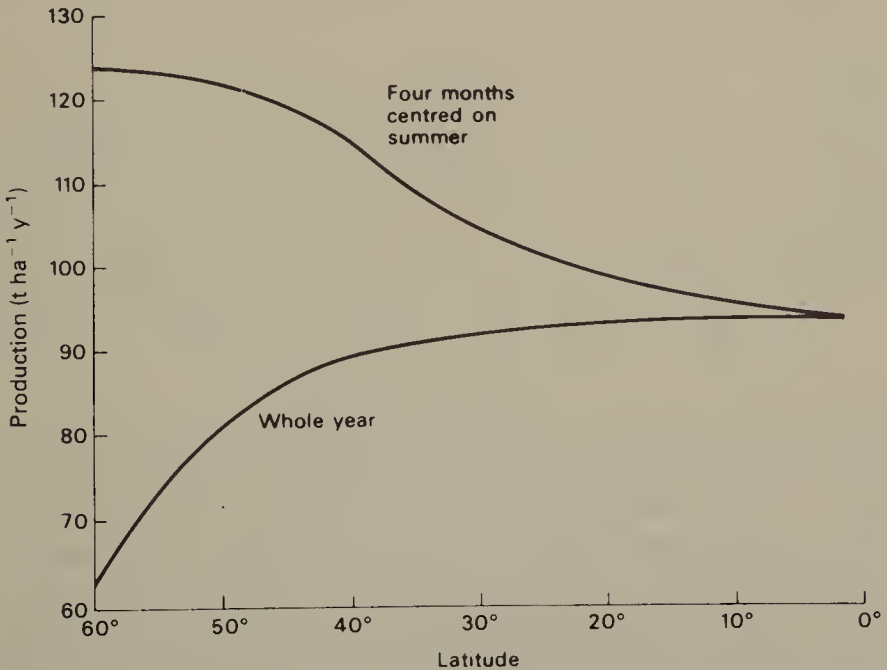
Figure 3.4 The latitudinal variation of potential net production rates in well watered vegetation.

cultivation especially – are the theoretical and actual net production yields approximately equal (Fig. 3.5).

The two major **limiting factors** to production are water in low latitudes and temperature in middle and high latitudes and mountainous areas. Some authors have attempted to derive maps of NPP from a consideration of these limiting factors. For example, Lieth (1983b) has proposed two models. The first, the 'Miami model', uses temperature and precipitation in mid-latitudes to predict NPP. As can be seen from Figure 3.6, this model gives an overestimate when compared to actual values of NPP in the natural vegetation. The limiting factors that prevent the achievement of the model prediction can be diverse but soil variations probably account for most of the shortfall. The second model applicable in low latitudes is the 'Manaos model', which relies on the length of the vegetative period.
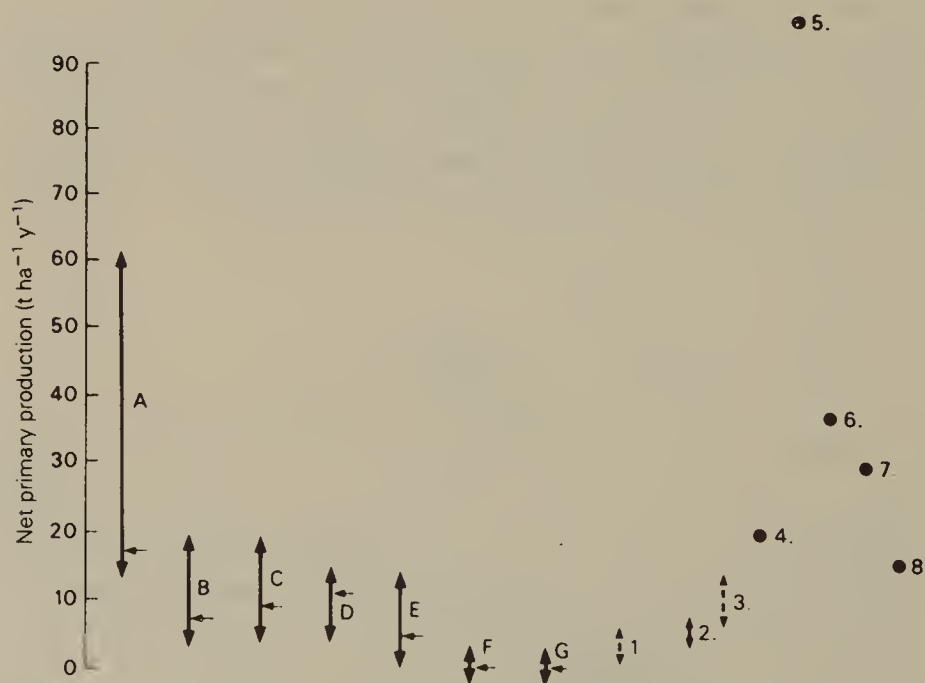
Figure 3.5   The variation of net primary production in various vegetation types. Natural ecosystems: (A) tropical rainforest; (B) tropical savannas; (C) boreal and montane coniferous forest; (D) deciduous forest of the Northern Hemisphere; (E) steppe grassland; (F) tundra; (G) arid lands (true deserts not recorded). The horizontal arrows indicate mean net primary production levels. Agricultural ecosystems: (1) lowland wet rice farming, Sri Lanka; (2) lowland wet rice, Bangladesh; (3) hybrid corn, USA; (4) lowland wet rice using 'high-yield' varieties, Vietnam; (5) sugar cane, Java; (6) oil palm, Congo Republic; (7) grassland, North Island, New Zealand; (8) Scots pine plantation, England. (Figures from various sources including Lieth and Whittaker (1975), Lemée (1967) and Leach (1975).)
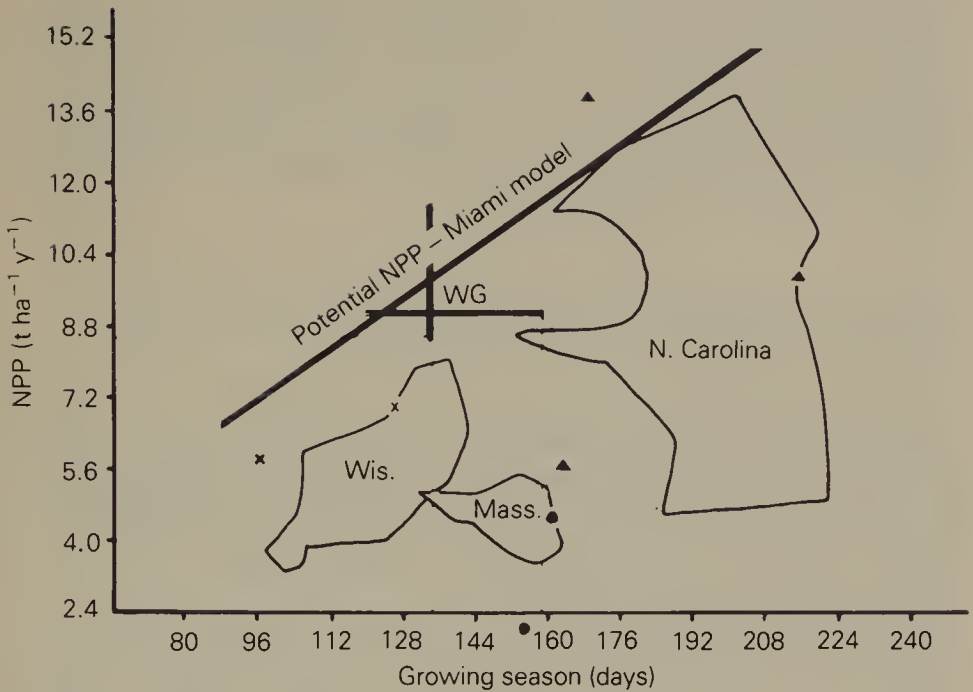
Figure 3.6 Diagram illustrating the discrepancy between actual and potential net primary production. Each enclosed area is based on the state counties' actual productivity. Counties with major discrepancy in NPP from the rest are indicated by isolated symbols. WG: the vertical and horizontal axes indicate the ranges of NPP in forestry and agriculture in West Germany. (After Lieth and Aselmann (1983).)

Reviews of productivity of natural vegetation (Jones 1979) have generally shown that estimates vary widely from one author to another for similar vegetation types. Figure 3.5 indicates the ranges quoted and the means for NPP. Some hope is offered that the confusion might be reduced by remote screening from satellites to estimate NPP on a continuous basis, but this is still in the future (Jensen 1983, Tucker *et al.* 1986).

The reasons why the actual and potential figures diverge so far in nature vary from ecosystem to ecosystem, but all of them can be summed up in the modern version of the agronomist, Liebig's 'law of the ̀minimum', which states that rate of growth is dependent on whatever factor in the environment is present in the. *minimum quantities in terms of need and growth* (Odum 1963). There are *no* environments in which some limiting factor or set of factors is not present. It may be a case of excessive shading, as in the dense rainforests, too little or too much rain, some mineral deficiency or any of the multitude of interacting components that make up an ecosystem.

Man's achievement since the invention of agriculture has been to trap an increasing proportion of the Sun's energy by eliminating or minimizing the effects of this law. He has done this by improving agricultural techniques and by evolving new breeds of plants with growth optima better adpated to lessen the checks that nature puts between actual and potential yields.

3.4   Plant response to the geographical variation of light

The seasonal and daily variations of solar radiation are a function of latitude and are of great biological consequence. Besides its effects on photosynthesis, other physiological activities vary in relation to the period of illumination, and these variations (**photoperiodic** responses) have been widely studied experimentally in relation to flowering, germination and growth.

In middle and high latitudes most flowering plants can be classed into long-day, short-day and indifferent plants according to whether they flower in response to critical day or night length. Long-day plants flower only in the late spring or early summer – the radish, iris, red clover, spinach, the smaller cereals and timothy grass are examples. Short-day plants flower in the late summer and autumn – tobacco, goldenrod, aster, dahlia, ragwort and chrysanthemum exemplify this group.

The dependence on day length means that long-day plants are excluded from low latitudes and that short-day plants may be excluded from higher latitudes as they may not complete their reproductive cycle before the first killing frosts arrive.

The selective force of day length is very powerful, and within particular species there may be ecological races adapted to different day lengths. In a classic piece of work, McMillan (1959) showed that the northern prairies of North America are dominated by long-day ecotypes that can take best advantage of the summer season, whereas the southern prairies are dominated by short-day or indifferent ecotypes. This goes far to solve the puzzle of how such a great span of latitude and therefore climate can be dominated by so few species.

For many years it was assumed that low-latitude plants would show little or no response to photoperiod variations. However, experimental evidence shows that they are, in fact, very sensitive indeed, possibly even more so than temperate plants. Thus over 14 tropical forest tree species have been demonstrated experimentally to grow faster under long-day conditions, some with growth rate

increments of over 200%. For some varieties of rice, claims have been made that differences of as little as *five minutes* in day length are detectable (Longman & Jenik 1974). The photoperiod response in tropical plants has also been shown to interact in a complex way with temperature changes, to which species also appear to be extremely sensitive.

It has also been widely demonstrated that both flowering time and seed production and germination are light-dependent in many species. Thus, in *Chenopodium album* two different types of seeds are produced related to the photoperiod of seed setting (Keresen 1970): small, black seeds are produced in long photoperiods, and large, thinner-walled seeds in short photoperiods. These seeds are differentially light-sensitive, the larger seed tending to have a low survival ability and rapid germination in light, the smaller, thicker-coated seed having a longer dormancy – up to an astonishing 500 years in fact (Ødum 1965) – and germinating only when light interacts with the hormone, gibberellin. The interaction stimulates the embryo sufficiently to enable it to disrupt the thick seed coating. This principle of long dormancy in thicker-coated seeds away from light applies to many early successional plants, and a number of authors have concluded that the initial stages of succession, especially by herbaceous plants, is best explained by *in situ* germination of dormant seeds rather than by colonization through migration to the site. Harper *et al.* (1970) suggests that angiosperm species are distributed on a continuum from *r*-selected types with small seeds capable of dispersing into unstable, early succession sites, to *K*-selected species with large seeds found in mature, climax vegetation. The former would have a long decay rate (biological 'half-life') and the latter a short decay rate. In complex tropical forests, not a great deal is known of the decay rates of seeds. However, work in the Costa Rican rainforests indicates that most of the seeds in the first 100 mm of soil were primarily of common pioneer species (Putz 1983). Work in the Panamanian rainforests also clearly indicates the rapidity of forest replacement when compared with that in temperate forests. A figure of 137 years was obtained for the main study area and 80–159 years in other sample areas (Lang & Knight 1983). In another instance in Costa Rica, Lieberman *et al.* (1985) discovered an area of moist tropical forest with a stand 'half-life' of as little as 34 years, one of the most dynamic replacement rates of any yet studied. Because the forest turnover is so rapid, it may be that the seeds of complex tropical forests do represent a continuum, as suggested by Harper *et al.* It is significant that pioneer species were only a majority

in the soil in the study referred to above, and seeds of climax species were also still viable.

The importance of uprooting trees in closed moist tropical forests as the major 'turnover' mechanism is emphasized by the concomitant rapid infilling of pits created. Figures of only 5–10 years are quoted, whereas in temperate forests pits may still be evident in the microtopography 300–500 years after the event. In tropical rainforests less than 1% of the surface may be pits and mounds, but in old temperate forests as much as 60% of the microtopography may be pits and mounds (Stephes 1956).

Of course, light is only one element of the total physical environment of a plant, and it is only relatively recently that experimental work has provided models to show how some of the various factors of the physical environment interact to influence plant growth. For example, work on *Trifolium subterraneum* (Charles-Edwards 1984) has shown that a hypothesis that the various meristems (growth tissues) of a plant require a minimum flux of assimilates to remain viable can be used to predict self-thinning in communities. Also Waun and Raper (1984) have modelled the classes of parameters for plant growth directly dependent on temperature and achieved results close to the predictions generated by their model (see also Sec. 5.1).

At local levels, the striking response that plants make to shade is of great importance in determining the structure of land plant ecosystems. Wherever a substantial cover of vegetation exists, the plants involved are subject to heavy shading for at least some parts of their lives and there can be few that do not react to this factor. Most are either shade-tolerant or shade-intolerant. In the natural development of temperate forests particularly, tolerance to light is usually a controlling factor in the progress of colonization and the establishment of species. It has been shown that, in the earliest stages of forest growth, it is the light-tolerant, high-producer species that become established on open sites. As their shade develops, it is the slower-growing, shade-tolerant species whose seedlings are the most successful (Fig. 3.7).

In the humid tropical lands, the structure of mature forests is closely related to demands for light. At the upper level are the emergents, which have evolved to take maximum advantage of the light available. In the middle and lower layers, there is intense competition for light, and the leaf mosaic, spread and arrangement of the leaf blades are usually closely related to available light. At the lowest levels are shade-tolerant shrubs and herbs, slow-growing saplings and seedlings (see Fig. 9.2).
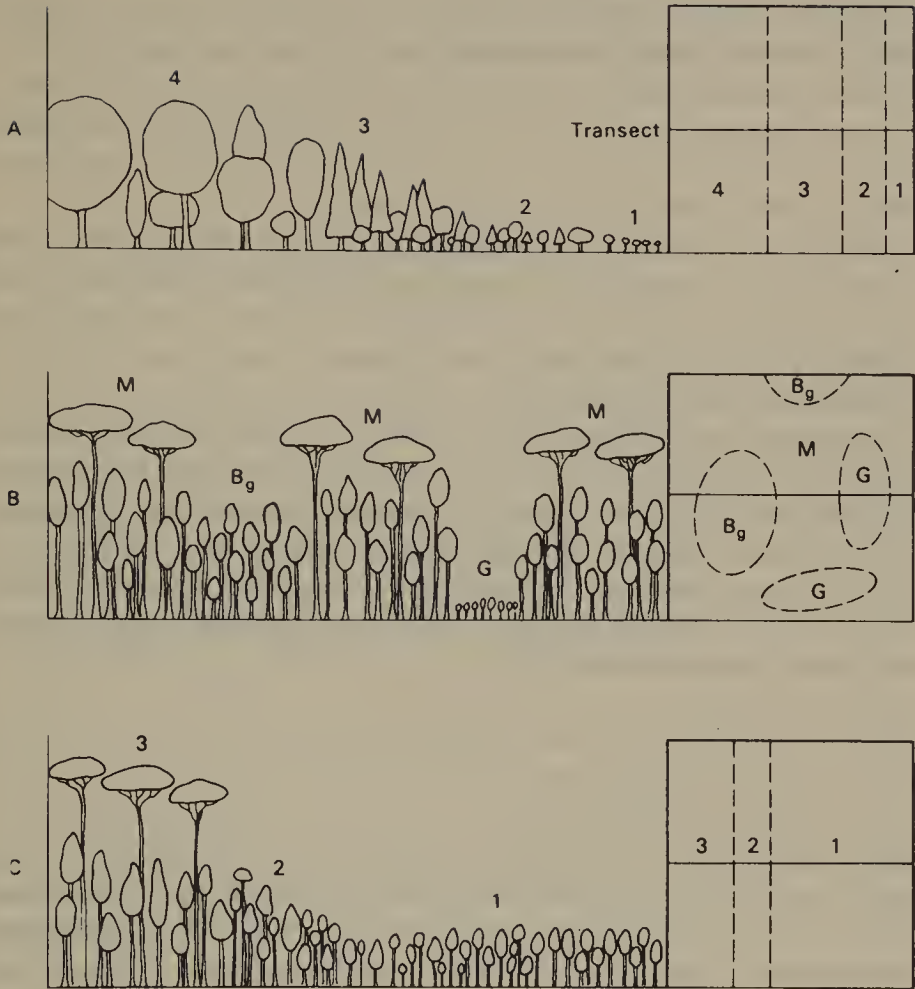
Figure 3.7 Three schematic models of successional patterns. (A) Model in middle-latitude temperate deciduous forest. This example was observed on old fields in Virginia. Phases 1–4 are from (1) high-producer species demanding much light to (4) low-producer, shade-tolerant species. (B) Regeneration pattern in tropical rainforest. In this model small gaps are quickly occupied from surrounding mature forest (M) to give a mosaic pattern of forest overall with gap phases (G) and intermediate building phases (Bg) recognizable in the areal pattern. (If the gap is too small, species needing most light may not regenerate.) (C) Regeneration into a larger area in tropical rainforest. Here succession from pioneer colonizers (which may include short-lived softwoods) with (1) light-demanding species to (3) mature forest may be recognized.

Studies have shown that these species are dependent on random sun flecks for their photosynthesis. These can provide on a clear day more than one-half of the daily photosynthetic flux density of understorey plants, suggesting a very rapid metabolic response by the leaf tissues to sudden illumination. This is all the more necessary as

only 18% of the waveband in shade can be used (Chazdon & Fletcher 1984). (See also Medina *et al.* (1984) and Uhl and Jordan (1984).)

The replacement of such forest with its many shade-loving species is a more complex process than the relatively simple model outlined above for the temperate forests. Thus it has been noted that, although there may be fully mature emergent species above, their seedlings and saplings are often absent below. These light-demanding species may not even regenerate when a gap opens in the canopy if it is too small, although in larger gaps covering several square kilometres a succession from pioneer colonizers to mature forest can be recognized (Fig. 3.7B & C).

The radiation to which plants respond by varying their growth rate is not necessarily that which they absorb for photosynthesis. There is good evidence that growth rate variations are considerably influenced by the balance of infra-red radiation received. This seems to be absorbed by a molecule called *phytochrome* and it is this that controls the growth response so that a plant reaches a suitable size in relation to the light conditions that suit it.

3.5   Energy microclimates

Plants participate in many more exchanges of energy with their environments than simply the absorption of radiation for photosynthesis and growth. They reflect radiation – some 10–15% of visible light in the case of a green field, 5–10% from a coniferous forest. They transpire water vapour, and heat flows to and from them by conduction and convection. Physicists have suggested (Gates 1980) that, to describe the true coupling of a plant to its environment, the energy microclimate (both input and output of energy) of the leaf must be accurately measured. Moreover, they have presented mathematical formulae for doing this and have suggested that this measurement of energy inflow and outflow could be extrapolated to whole forests.

As may be imagined, the complexities of such a task, desirable though it may be, have not encouraged many workers to accept the challenge. Moreover, plant growth and behaviour can be correlated with other energy-related factors in the environment, such as temperature, evaporation and light variations. These can be applied at both the microclimatic and macroclimatic levels and have the advantage of being easier to measure. Thus the familiar climatic statistics, however suspect in the eyes of a physicist, still have relevance in describing the

energy microclimate of plants. Moreover, their usefulness has been considerably enhanced by the development of models whereby, using standard environmental data, productivity patterns can be predicted (Lieth & Whittaker 1975).

3.6   Energy, land plants and geomorphology

The amounts of energy that flow to and from the habitat of a community and the individual plants which compose it, and from one community to another community, in time considerably modify the nature of the habitat itself. A soil that develops on a bare rock surface is a material very different from its parent rock and one which is in dynamic relationship with the organisms it supports. Energy is supplied to it by leaf fall and dead plant and animal material. Its chemical and physical structure is dependent on that energy supply being maintained. Once it is cut off, its nature radically alters.

The fixed energy in the form of the plant **biomass** (the weight of organisms involved in an ecosystem) also alters the habitat near the ground. It controls the way in which rain is received and distributed back to the atmosphere and runoff, and it modifies wind speed and controls insolation and radiation. Consequently many geomorphological processes operate very differently from the ways in which they affect unvegetated surfaces. One has only to consider the vastly accelerated erosion rates consequent on deforestation or the ploughing of some grasslands to realize the erosional energy that plants divert by their presence.

Until recently the precise effects of the energy exchanges within ecosystems on the processes of earth sculpture were not well understood. That these effects are profound cannot be doubted. It might not be too sweeping a case to argue that, as the activities of green plants have largely determined the atmosphere's present composition and strongly influenced the distribution of energy within it, then precipitation and runoff must, as agents of earth sculpture, be seen as functions of the biosphere.

The system of energy flow briefly outlined in this chapter has been going on for 2500–3500 million years. The exchange of gases and materials facilitated by it has enabled plants to create of this planet's oceans, atmosphere and land surfaces a world almost literally fashioned in their own image, a 'meadow in the sky' as one poet has put it. The results of the recent exploration of the Solar System have brought home to us how different is the Earth from its dead

neighbours and how much of this difference in its outer biospheric skin is due to the dynamic energy flux which is life (Siever 1975, Lovelock 1980).

3.7   Production in artificial ecosystems

Few agricultural systems, however efficient they may be in trapping the Sun's energy during the growing season, can outperform natural systems on an annual basis. Even where attempts to avoid 'the law of the minimum' are intense, as with heavy use of fertilizers in industrialized countries, the results may barely justify the means in energy terms. Heichel (1973), for example, showed that the output of digestible energy from oat and soybean farming in the US Mid-West was barely above that of the same lands producing maize in 1915 in spite of the much greater energy inputs needed to sustain the system (see also Slesser 1975). This is not to say that high energy expenditure is unnecessary within current western farming practices. Indeed, these systems, as also the new 'green revolution' crops of the less-developed world, would be unsustainable without them. What it does suggest is that the true costs are rarely well understood. Cost–benefit analyses that ought to reveal the true costs are constrained to the too narrow limits of immediate input–output analysis of the cropping itself.

Figure 3.8 illustrates how many energy inputs can be involved. The total costs in energy of the right-hand boxes are rarely taken into account in analyses of the economics of farming systems. The diagram also reveals the simplicity of subsistence farming systems and it might be expected that, on good soils with ample rainfall, these systems would be more efficient in energy terms (Oldfield & Alorn 1987). Rapaport (1971, 1976) has clearly shown how efficient these systems can be in wet, tropical forests (see Sec. 9.4).

The dilemma presented by these two aspects of the diagram is obvious. On the one hand, subsistence systems may be energy-efficient but are not capable of the large outputs necessary to sustain growing urban populations (nor of generating rising living standards comparable to those of the industrialized world). On the other hand, large-scale mechanized agriculture is energy-inefficient but can generate the large-scale food surpluses essential for feeding populations that have left the land. Given that the peoples of the world today are dependent on one or the other of these systems, what steps can be taken to improve the ability of these systems to convert
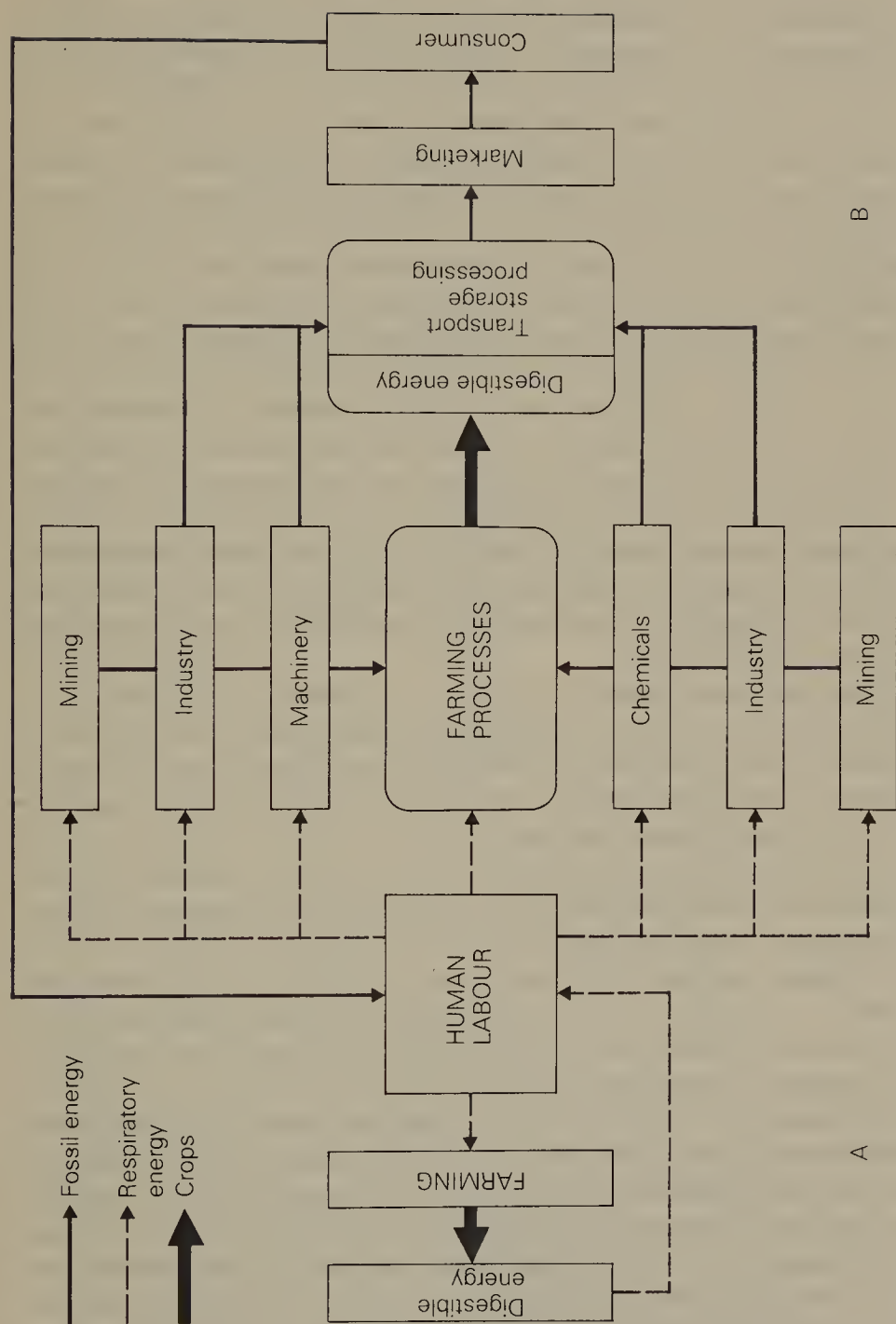
Figure 3.8 Energy inputs to industrialized and subsistence farming systems: (A) subsistence farming; (B) industrialized farming.

radiant energy to food? The answers to this question are far beyond the scope of this book, but from the examples of India and China, particularly, it is probably a far easier task to improve the efficiency of subsistence systems than of industrialized ones. Both these countries have shown that human labour systems can be highly productive and, as relatively few people have left the land as yet, the artificial energy inputs to cultivation and fertilizer usage need not be excessively large to produce a significant increment of digestible energy and concomitant disposable wealth. With mechanized agriculture, no such relatively direct pathway to increased efficiency is open. The technological sophistication of these systems has removed them so far from natural patterns of production that they can only be sustained by a complex of scientific and industrial expertise; new crops, new crop protection chemicals, new machinery and new processing systems are constantly required to sustain the levels of production achieved or to increase them. Moreover, the systems are so firmly keyed into the social and industrial fabric of these societies that even applying true cost remedies would produce unacceptable social and political consequences. For the foreseeable future they will continue to exist, supported by overt or hidden subsidies from the industrial communities they feed.

That such systems can be deleterious to even very good soils such as those in Great Britain is undoubted. The Soil Survey of Britain has warned that soil erosion, although not on a large scale, is widely detectable in British soils at rates well beyond the rate of regeneration (Morgan 1985; see also Sec. 6.6).

Productivity figures for sylviculture are not abundant in the form of NPP rates, the forester being more concerned with volume production figures for usable wood.

Estimates suggest that approximtely 30–35% of the assimilated matter in temperate trees is harvestable, representing less than 0.5% of the total incident radiation (Lieth 1983b). This compares with 30% for potatoes and only 4% for cattle systems. Over time, forestry in the westernized world (except the USA) has become conscious of the limitations to production posed by habitat factors and tree varieties, as the many publications of the national forestry bodies testify. The care taken in Sweden, for example, in tree breeding for maximum production goes back well beyond the half-century and forestry on a sustained-yield basis is highly efficient. In tropical lands, on the other hand, sustained-yield forestry is in its infancy, although there are some long-standing examples, as in Malaya where mangrove plantations have been rotationally cropped for a number of decades. As yet

only 2% of the moist tropical forests have been converted to plantations (Myers 1980), but the potential is known to be enormous. At present, the genera that are planted there are overwhelmingly either *Eucalyptus* spp. or Caribbean pines (38% and 34%, respectively), some 14% is teak and the rest other tropical hardwoods (*Acacia* spp. and *Gmelia* particularly). In contrast to temperate forests with a production averaging around 10 m^3 ha^{-1} y^{-1}, the tropical moist forest plantations yield around 25–35 m^3 ha^{-1} y^{-1} and in some eucalyptus stands as much as 60 m^3 ha^{-1} y^{-1}. These figures should, however, be treated with caution. Jordan (1983) has gathered evidence to show that the widespread view of tropical moist forest plantations as highly productive of wood may be incorrect, and natural forests away from coasts may be no more productive of wood than temperate forests.

Although many tropical hardwoods have been used over a long period for furniture, veneers, etc., their strongly lignified tissue is only now being appreciated for its potential as constructional timber. Some of these woods have an engineering performance half that of mild steel but as yet their use is limited in spite of other desirable qualities they possess, such as their resistance to fungal infection and water penetration.

In spite of the advantages of plantation forestry in tropical lands, much of the timber produced still derives from destructive logging practices, even though only some 5% of the natural forest wood is extracted as commercial timber, and it is only recently that management techniques for forest reserves have been formulated. In areas like Amazonia, where active clearance is taking place, the sizes of 'island' forest reserves are critical to maintain their viability. Lovejoy *et al.* (1983) have shown that in reserves of less than 10 ha trees cannot reproduce themselves and in 'islands' of less than 100 ha most of the mammalian fauna cannot survive.

In temperate lands, particularly Europe, the native hardwood and even softwood types were selected as survivors by the Pleistocene glaciations. As Lechowicz (1984) has pointed out, they have been 'decoupled' from their original ecological niches and in their present habitats are in 'evolutionary disequilibrium'. Consequently, the forester who is seeking maximum productivity must search amongst the world's stock of species to find trees able to maximize NPP and accumulate growth within the site conditions of their designated new habitat. The Forestry Commission of the United Kingdom has been particularly assiduous in this task, faced as it was at its inception in 1918 with only 2% of the surface of the country in forest.

Up to the 1950s it was thought sufficient to know only the region of seed provenance to find suitable types. Since then, research has shown that site matching of source of seed and production can give greatly enhanced results. Thus in the western seaboard of Britain, a subtype of Sitka spruce (*Picea sitchensis*) from particular areas of Queen Charlotte Island (Western Canada) performs best (Jones 1979).

There is little doubt that, given the political will, timber production in the tropical lands especially has enormous potential for increasing the world's wealth while at the same time conserving the world's biotic stocks. Research expertise and information resources are increasing rapidly, especially in relation to tropical lands. (Between the first and second editions of this book, for example, the amount of research literature on tropical vegetation has increased considerably.) Unlike agricultural ecosystems, sustained-yield forestry has the advantage of an energy dynamism that parallels natural ecosystems. This gives concomitant benefits in its preservation of essential homeostatic tendencies in the disposition of energy in the environment, particularly in relation to the vital soil resource. However, whether these hopes prove to be pious rather than realistic remains to be seen. The reader will find in Melillo *et al.* (1985) figures of forest removal in the tropical world which suggest that the timescale for any rational policies to be adopted is very short indeed.

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4

Nutrients and nutrient cycles

Because it is ultimately dispersed back to space as heat, energy flows in only one direction through an ecosystem. In contrast, the materials from which living matter is fashioned are in constant circulation back and forth between plants and animals and the non-living environment.

4.1 Biogeochemical cycles

The quantities of materials (nutrients) required by living matter serve to distinguish two main groups: macro–nutrients and micro–nutrients. The former comprise water, oxygen, carbon dioxide, mineral nitrogen, sulphur, phosphorus, calcium, magnesium and potassium. The latter include iron, manganese, boron, copper, zinc, vanadium, cobalt, molybdenum and possibly many other elements required by particular species.

All the materials are simple inorganic elements and compounds (biogenic salts) derived from rocks, water and the atmosphere. Once involved in an ecosystem, these nutrients follow pathways of greater or lesser complexity called biogeochemical cycles, set out schematically in Figure 4.1. Apart from water and the gases, only small fractions of the total nutrients in circulation ever escape once they are part of a stable ecosystem.

Figure 4.1 indicates that nutrient cycles are of two types, atmospheric and sedimentary. The two types may be illustrated by comparing briefly the nitrogen and phosphorus cycles (Fig. 4.2). Both elements are needed by plants and animals in relatively large quantities, nitrogen being essential to the formation of amino acids (the building blocks of proteins) and phosphorus to the energy metabolism of living matter. Like all nutrients, whether needed in large quantities (macro-nutrients) or as traces (micro-nutrients), their availability to green plants depends on a host of micro-organisms and
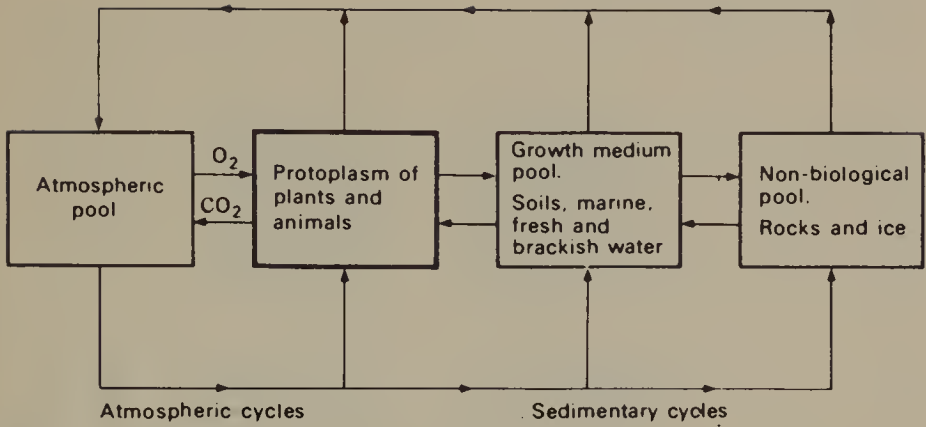
Figure 4.1   Simplified model of nutrient cycles.

animals, the circulation of the oceans and atmosphere, and global and local geological processes (see Holland 1984). The various stages involved for these two elements are set out in Figure 4.2.

Because of the importance of microbes in mineral element circulation, the climatic and other conditions that determine the circumstances for growth of micro-organisms will have important effects on the nutrition of higher plants. Thus, in cold, wet soils the bacterial populations will be low, including those with the ability to fix atmospheric nitrogen, and as a result the soil will be deficient in nitrogenous compounds such as nitrate. Organic matter may also accumulate because of its slow destruction. It is on soils like these in Britain that the bizarre plants like sundew (*Drosera* spp.) and butterwort (*Pinguicula* spp.) occur, obtaining their nitrogen from the digestion of insects. Cost–benefit analysis of carnivory in tropical plants, particularly the bromeliad, *Brocchinia reducta*, has clearly shown that carnivory is advantageous only in moist, nutrient-poor habitats (Givnish *et al*. 1984). In warmer climates, on the other hand, humidity favours both the fixing of mineral nitrogen and its rapid release from organic compounds. Where soil acidity is high, the rates of both humus formation and mineralization are usually poor, while alkaline soils discourage mineralization but encourage humification.

Climatic and soil-forming processes may also have important effects on a mineral like phosphorus. Free phosphates are very likely to become tightly bound to clay minerals, especially kaolinite. As this mineral is usually an abundant product of the rock/soil weathering process in the wet tropics, there may be little phosphorus available to plants from the soil. Most of what is available is usually locked into the living biomass and reabsorbed rapidly on its release by decay before it can be bound into the clay minerals. Thus, although

Figure 4.2 Nitrogen and phosphorus cycles compared. Note the importance of micro-organisms in both.

nitrogen and phosphorus circulate via different pathways, they are available to land plants only through the medium of the soil, and this is true of all the other nutrients except carbon and oxygen.

It is useful to gauge how efficiently nutrients are used in vegetation, in both domesticated crops and natural vegetation, as the efficiency of nutrient use has important effects on the natural biogeographical cycles. (Nutrient use efficiency indices are obtained from the rati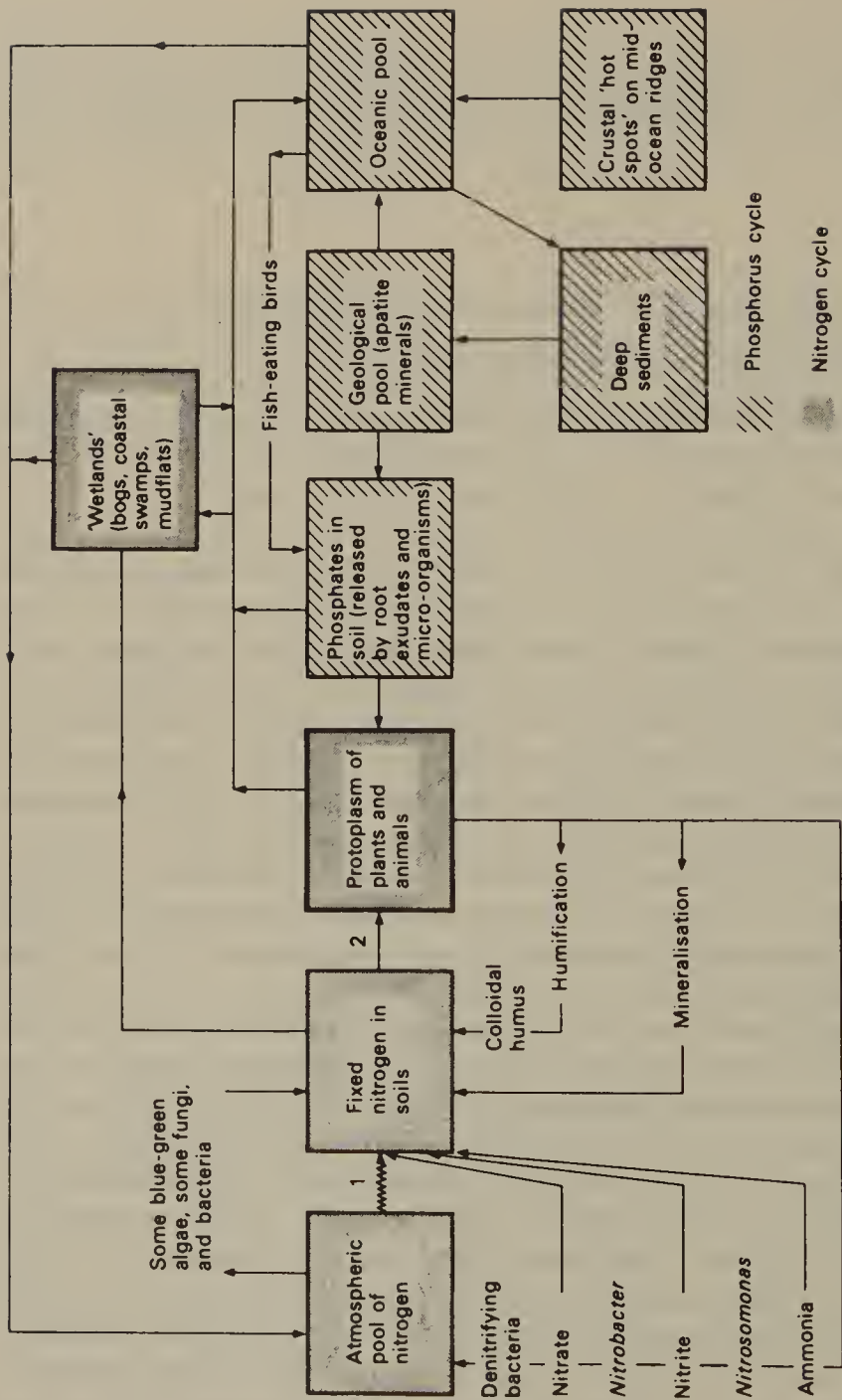o of net primary above-ground production to unit of nutrient available.) It has been found, for example, that nutrient use efficency is greater on nutrient-poor sites than on sites with plentiful nutrients (Vitousek 1982). Also, there is now a good deal of evidence to suggest that, in many vegetation types, for example wet, tropical forest, there is a negative correlation between species richness and fertility (Huston 1980). Adoption of species to give highly efficient nutrient use on nutrient-poor sites in managed systems thus presents problems if production is to be increased using fertilizer. For example, Cole (1981) has shown that temperate ecosystems are widely deficient in available nitrogen, and Birk and Vitousek (1986) have demonstrated that the addition of nitrogen fertilizer to increase production in semi-natural woody vegetation is far too simplistic a solution. In their study area in southeastern USA, the addition of nitrogen fertilizer to the nutrient-poor site occupied by semi-managed loblolly pine stands had almost no effect on production. The plants were well adapted to low nutrient availability and highly efficient nutrient use. The major result was an increase of weedy, herbaceous vegetation, which took up most of the added nitrogen. The workers concluded that only extensive and expensive weed clearance might increase production and that, if the stands were left without fertilizer or weed clearance, they would perform almost as well in any case.

Although the full scale at which biogeochemical cycles operate is global and their timescale geological, within a short time mankind has had striking effects on both atmospheric and sedimentary cycles. We have added measurably to the atmospheric cycle by burning fossil fuels, and we have increased the rate of circulation of the sedimentary cycle by deforestation, agriculture and mining. Combustion and industrial chemical processing release to the atmosphere vast quantities of carbon dioxide, carbon monoxide, sulphur dioxide, hydrogen sulphide, nitrogenous compounds and hydrocarbons. Most of these, except sulphur dioxide and hydrocarbons, are released in smaller quantities than from natural sources. However, even where the natural source is enormous, the effects of pollution may be detectable.

A number of authors have concluded (Berner 1982) that world-wide cycles of nutrient elements have been perturbed to a significant extent by human activities. In the case of phosphorus, for example, estimates suggest that total world river load of diluted (pollutant) phosphorus is around 0.4×10^{12} g y^{-1} (Meybeck 1982). This study also shows that a close correlation can be made for carbon, nitrogen and phosphorus transfer with an index for consumption of energy, the Valentyne demographic index. This indicator of population energy consumption is derived from the ratio between per capita energy consumption over a given period and the energy required to satisfy basic human needs. It can vary from less than 1 in some less-developed countries to over 90 in the USA (Valentyne 1978).

It has also been noted that the mean carbon dioxide content of the atmosphere has risen from 275 ppm in 1880 to 339 ppm in 1980. The increment in the atmospheric content of this gas particularly has given rise to much dire forecasting of its eventual effect on the Earth's heat balance, as CO_2 is opaque to outgoing long-wave radiation, which it absorbs, so raising its temperature. This effect has now been shown to be a reality (US DOE 1986, Houghton 1987). It has also been discovered that other gases in the atmosphere play a part in the Earth's atmospheric heat budget. Thus methane, N_2O, O_3 and chlorofluorocarbons together contribute approximately half as much again as carbon dioxide to the so-called 'greenhouse effect' in the Earth's atmosphere (Abelson 1986). As we have seen (Sec. 2.5), there is some evidence that a greenhouse effect may have occurred in the geological past, but whether the current rise in pollutant, heat-retaining gases will produce the higher temperatures that some scientists have forecast is not known. However, it has long been known that plants respond to increased atmospheric CO_2 by increasing their growth rates. Evidence has been presented that this response is now detectable in natural vegetation in the thickening of tree rings (Lamarche *et al.* 1984).

Carbon monoxide, which until recently was regarded as being present in relatively stable amounts in the atmosphere in spite of the vast quantities emitted from fossil fuel burning, has now been detected as having an increasing trend also (Khalil & Rasmussen 1984).

These atmospheric pollutants have already had marked responses in some vegetation types and have considerably altered the patterns of biogeochemical cycling. For example, in the eastern USA, the uptake by canopy leaves has been shown in some cases to supply the bulk of the annual requirement for some nutrients and significant

proportions of the requirements for others. These nutrients interact with the forest canopy in two main ways: sulphur, nitrogen and free acidity (H^+) are absorbed as vapour, and calcium and potassium are deposited as particles. The last two tend to be washed off the leaves but the vapour uptakes are tightly held. In the particular forest studied, atmospheric deposition supplied 40% of nitrogen and 100% of sulphur requirements for annual woody increment. The workers who carried out this study (Lindberg *et al.* 1986) also noted that standard bulk deposition collection methods significantly underestimated the contribution of these pollutants to ecosystem nutrient budgets. They also pointed out that, as the levels of air pollution rise, many of these elements will be supplied to excess, and that high-level vegetation in the eastern USA and Europe, especially, may be the first to demonstrate those effects (Hinrichsen 1987). In other regions away from heavy atmospheric pollution, the supply of nutrients by filtration from the atmosphere does not seem to be of major significance. For example, one study carried out in Belize on *Pinus caribaea* plantations showed that, while the canopy was an effective filter for nutrients, only potassium from the atmosphere was adequate for the growth demands of pine. Calcium, magnesium and phosphorus interception were well short of need, and these were supplied by the limited nutrient stock in the rather poor soils of the site studied (Kellman & Carthy 1986). Natural vegetation has been advocated by some workers (Cole & Smith 1984) as a clear 'early warning system' of type and intensity of damage by environmental pollution.

In many parts of the world, deforestation and farming are adding nutrients to the oceanic sinks. Eroded material from the land masses accumulate ultimately to form sedimentary rocks. Once incorporated in these geological sinks, these nutrients will be lost for millions of years. Phosphorus, for example attached to clay minerals swept away in rivers, has to be replaced by the mining of phosphatic rock taken from the geological sink. This may be lost very quickly back to the oceans.

The nature of nutrient use in farming and other artificial ecosystems is, in fact, qualitatively different from their natural circulation. It is more akin to the flow of energy in an ecosystem in that it is largely one-way and parallels the flow of energy. As energy flow in artificial ecosystems increases, so does the throughput of materials with it.

The effects of nutrients washed from the land in excess of the natural flux is particularly detectable at the air/sea interface. This

boundary layer is extremely narrow (30–100 μm) and is a very high-stress biological niche in which the micro-organisms are adapted to withstand and tolerate high ultra-violet radiation and high pollution levels. Their resistance to pollutant contamination allows them to absorb enhanced amounts of contaminants when compared to bacteria at lower depths, and thus almost any pollutant is incorporated by them into the food chain. Moreover, they are passed from the sea to the air across the boundary layer by ejection of water droplets from breaking waves and can be found in these droplets at up to 1000 times their concentration in bulk liquids. As these droplets can be carried up to 30 miles inland, pollutant toxic chemicals, for example radioactive materials, can quite quickly return to the land (Lion & Leckie 1981). This effect will be enhanced if pollution occurs in nearly enclosed seas or estuaries. The cycling of mineral nutrients from plant to soil and back again is only partially understood, but many studies have shown it to be a complex process, with wide variations in details from one vegetation type to another, from one type of litter to another, and with considerable variation induced by the type of soil fauna and flora.

Figure 4.3 illustrates the varied pathways for some of the nutrients in beech forest leaf litter in southern Sweden. These pathways, however, cannot simply be extrapolated to other deciduous temperate forests. Conditions will act to vary the processes from place to place. The varied site conditions – soil, climate and so on – are most faithfully reflected in their effects on soil fauna and flora, which play such an important role in mineral cycling. In temperate deciduous forests, the various tropic balances between these are shown in Figure 4.4.

Proctor (1983a, b, 1984) has shown how little is firmly known of both production and mineral cycling in tropical forests. Consequently, Figure 4.4 cannot be applied to tropical systems, where the role and balance of all the soil fauna and flora may be quite different. In many tropical lands with large termite populations, the macrofauna would play a proportionately greater role in the pattern of recycling. Studies in the savanna lands of Nigeria have shown, for example, that Macrotermitinae take 60% of the annual wood litter, 60% of the grass litter and 3% of the leaf litter, in total 35% of the total annual litter in vegetation type. The process is dependent in turn on the symbiotic fungi cultivated by these animals (Collins 1981). As a result of this high productivity, fungus-growing termites are central to many predatory food chains, ants, birds and even human beings.

The reabsorption of nutrients, once present in soil water in

Biological
mineralization
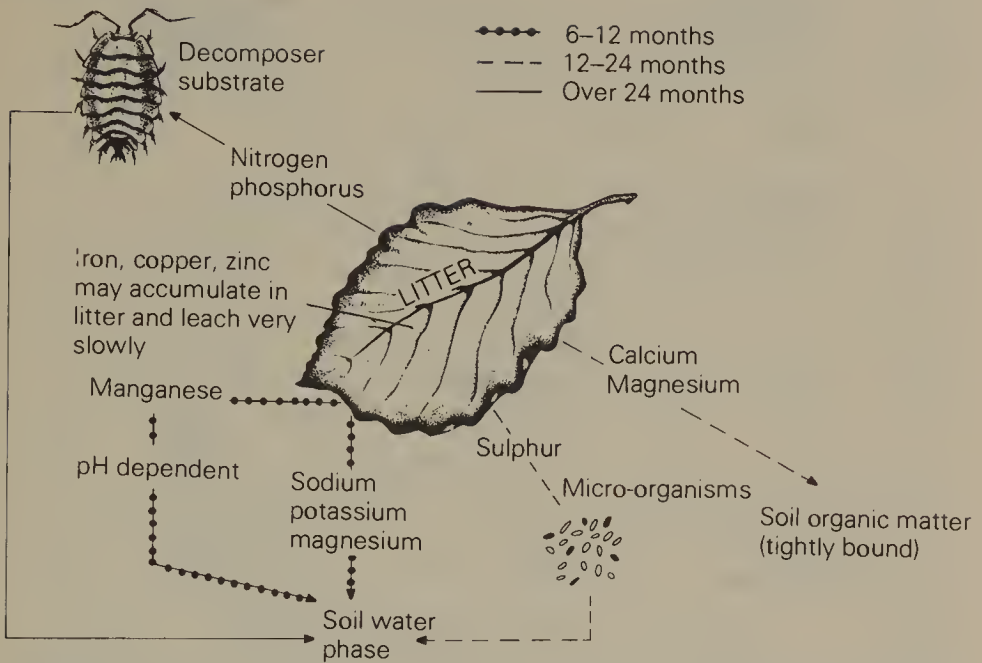
Figure 4.3 Release of nutrients from leaf litter in southern Swedish beech forest litter. (Data from Staaf (1985).)

available form, is not necessarily a simple process. The intervention of micro-organisms may be equally important in this process. Studies have shown that fungi that infest the root and spread out into the soil (called *ectotrophic mycorrhizal fungi*) play an important part in nutrient absorption in many higher plants. These fungi are able to absorb simple organic materials, for example peptides and amino acids, and evidence shows that they are able to supply the higher plant with other nutrients such as phosphorus, sulphur and zinc (Pate 1983). Indeed, where ectotrophic mycorrhizae **horizons** are profuse in the soil, the vegetation is likely to be nitrogen-stressed, and the **mycorrhizae** are likely to be abundant in any nitrogen-rich surface layer. Thus, in cool temperate deciduous forest, boreal, montane, arctic–alpine and mediterranean environments, most trees will have mycorrhizal symbionts. In some waterlogged, acid, peat soils, plants such as *Vaccinium* sp. may lack the ability to absorb nitrogen completely and be entirely dependent on fungi for a supply of this nutrient. Although mycorrhizal nutrition in tropical plants has been shown to be important in orchids, it has not yet been proved to be important in tropical trees, although there has been much speculation
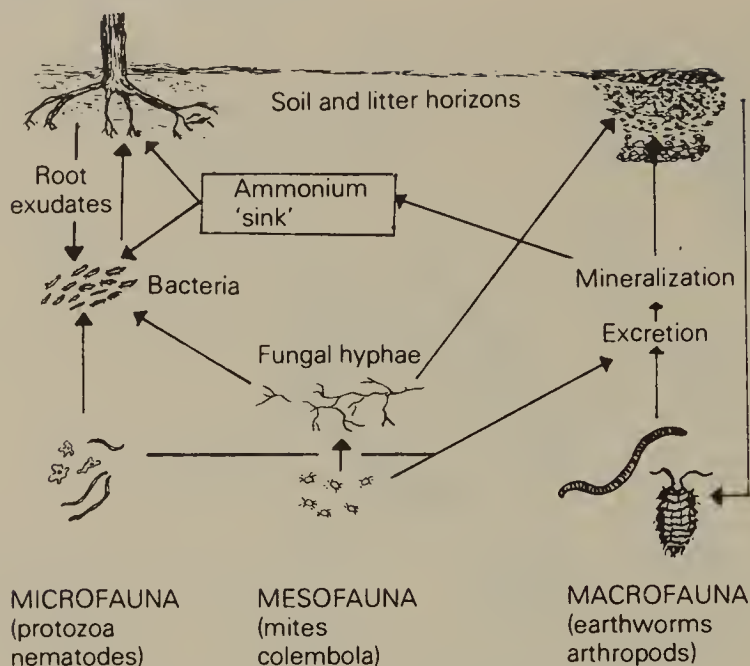
Figure 4.4   The role of soil fauna and flora in detrital mineralization.

that it may be. Janos (1983), for example, argues that tropical tree mycorrhizae lack the enzymes necessary to mineralize litter.

Intervention by other organisms may be involved in some environments. For example, in sub-arctic woodlands, the lichen layer has been shown to be an important source of fixed nitrogen if the plants contain blue-green algae. This has been demonstrated in the lichen *Stereocaulon* (Crittenden 1983). Blue-green algae have also been shown in temperate soils to be an important source for fixed nitrogen (Sec. 11.4).

4.2   Nutrient groups

In addition to the macro- and micro-nutrient groups listed at the beginning of the chapter, there may be many others that plants can absorb which have poisonous (toxic) effects. In fact, almost *all* of the otherwise useful nutrients may be toxic to a particular species, or, if they are present in excessive quantities or in certain combinations, to a variety of species.

Plant pathologists have clearly shown that nutrient supply has important applications for the control of disease in higher plants. Thus, nitrogen in great abundance may predispose a plant to

pathogen attack and micro-nutrient deficiency. As micro-nutrient deficiencies in particular can predispose plants to disease, it is not surprising that, given the enormous quantities of nitrogen fertilizer used over the last 100 years, cultivated plants especially are vulnerable. This is the result of a shift in the host–pathogen balance from the historical or evolutionary past.

Not only are cultivated plants more liable to attack through the nature of nutrient supply, but they also differ from wild types in their response. The latter when faced with a deficiency of nitrogen usually produce long, thin roots with which to explore the environment for a nitrogen supply and translocate nutrients from old leaves to supply the meristems. Most cultivated crop plants appear to have lost this ability in their breeding to employ 'active' responses to overcome or minimize soil nutrient limitations to production and growth. In particular, deficiency symptoms for iron, boron, manganese, zinc, calcium, molybdenum and copper can appear frequently in the young tissues of cultivated plants, which would not be obvious in wild plants growing in the same soil.

In general, nutrient-deficient plants have less chance of surviving pathogen attack, but in cultivation the addition of particular mineral nutrients has been shown to confer often dramatic enhancement to disease resistance. For example, experiments with powdery mildew infection of barley (Last 1962) showed that the addition of nitrogen to the substrate had the effect of enhancing growth but decreasing resistance. Moreover, the additions of phosphorus decreased liability to disease but only when administered in optimal amounts. However, the addition of potassium dramatically increased disease resistance. The same effect has been found with even minute amounts of trace elements, for example silicon, aluminium, lithium, chromium, iodine and fluorine.

Figure 4.5 indicates the total amounts of mineral nutrients in litterfall circulation in some of the major vegetation types for which figures are available. Probably the most striking feature of the diagram is the enormous quantities of mineral elements in circulation in the tropical rainforests. This is not solely a direct relationship to mineral availability (due to the rapid rate of nutrient release by weathering) and the opportunity for high production, although this accounts for most of the difference. It is also a function of the relative lengths of time during which the biogeochemical cycles have been operating comparatively undisturbed on these surfaces. As we saw in Chapter 2, almost every other vegetation type, with the possible exception of the subtropical forests, has suffered considerable dis-
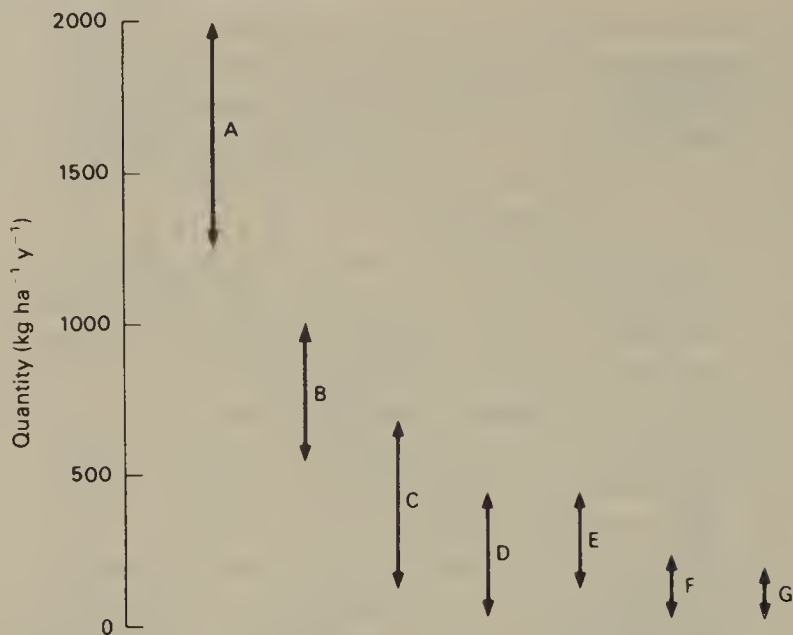
Figure 4.5 Range of mineral element quantities in litterfall circulation in various vegetation types. The predominant element in the litter is also given. (A) Tropical rainforest (Si 50–60% of leaf-fall ash); (B) subtropical seasonal forest (Si plus N in some); (C) mid-latitude steppes (Si); (D) desert communities (Cl in solonchak soils; Si in semi-shrub desert with annuals); (E) mid-latitude deciduous forest (Ca); (F) coniferous forest (Ca; see Fig. 12.1); (G) tundra communities (N). (Data from Rodin and Bazilevich (1967).)

turbance during the last two million years, so that mineral cycles in many higher-latitude environments have been in operation for only a short time. If it were possible for us to measure the mineral cycles of the Arcto-Tertiary forests, they would almost certainly be on a greater scale than those of their impoverished descendants today.

Figure 4.5 also indicates that the predominant minerals shed with the litter vary widely from one type of vegetation to another. Some of these minerals, for example silicon and chlorine, may in most cases hardly be 'nutrients' in any important sense at all and have little more than nuisance value to the plants, which pass them back and forth. (There is some uncertainty about nutrients of this kind, however. For example, silicon has been shown to be important in the metabolism of rice and in savanna grasses. See. Sec. 10.3.)

The reason why plants cycle large quantities of minerals of possibly limited utility lies in the way they absorb minerals from the soil. Most plants are fairly indiscriminate in their mineral nutrition, taking elements from the environment more or less in the proportions in which they exist in soil water. It is for this reason that plants can

easily be contaminated by man-made pollutants like toxic metals and radioactive fallout.

The amount of sampling information now available following the intensive work done by the scientific community in the middle decades of this century is now such that a reasonably accurate picture can be given of the general global circulation of many of the macro-nutrients (Meybeck 1982). Further details at scales from the local to that of a major region are constantly being added, particularly for tropical lands. It is also possible to discern within large regions the effects of human interference in natural nutrient cycles. For example, in West Africa, the regional cycle of nitrogen has been shown to be only slightly affected by the direct fluxes from farming but very markedly influenced by indirect effects due to forest clearance (Robertson & Roswall 1986).

4.3 The geographical variability of nutrients

The variation from place to place of mineral and other nutrient supplies has been one of the most potent factors in plant evolution, and many of the major and minor varieties of vegetation type can be ascribed to it. By the evolution of species that can patiently hoard scarce minerals, plant life can overcome many of the obstacles to production in habitats where certain minerals are hard to obtain. By their tolerance of what to other species may be toxic minerals, certain species may gain enormous territorial advantages. For example, the genus *Fouquieria* (the 'gypsum flower') in the arid zone of northern Mexico can dominate large areas of gypsum soils by its tolerance of SO_4^{2-} ions. Indeed its growth is limited to such media.

The ability of plants to adapt to media containing excessive amounts of particular nutrients can be of considerable practical value in mineral prospecting in many parts of the world, the presence of particular species or varieties revealing the near-surface presence of metal ores particularly (see Brooks 1983).

However, by far the most potent factor in plant evolution in relation to nutrient supply is that of water. Hoard it as they may, plants need to breathe and photosynthesize, and this implies water loss by evaporation at some time or other.

Unlike many of the other materials that can be circulated almost indefinitely in a well established ecosystem, the renewal of water depends on the global circulation of the atmosphere and the oceans. Driven by the solar energy budget of the Earth, it is outside the

control of the individual species composing the individual ecosystems. In middle and low latitudes, the energy conditions of the atmosphere are such that low relative humidities and high evaporation rates may be expected at some time in almost every habitat including the tropical rainforests. Thus, water supply is a major determinant of the individual characteristics of species and the geographical pattern of vegetation. Even in high latitudes with plentiful water and low evaporation rates, plants experience difficulties of supply during the year owing to the slower rate of flow of water and the sluggish behaviour of protoplasm at low temperatures. Water supply is of such fundamental importance to understanding the geography of plant life that it will be dealt with at greater length than the other nutrients.

4.4   Water supply, plant metabolism and geographical pattern

Water is the medium in which the hydrated organic molecules of protoplasm are bathed; it participates in numerous chemical reactions, not least photosynthesis; it acts as a solvent and transporting medium; and it maintains the form of non-woody tissues. Notwithstanding all these vital functions in plants, most of the water that is absorbed is never used. In maize, for example, 98% of the water absorbed is lost and only a minute fraction, some 0.2%, is used for photosynthesis.

Just as with mineral nutrients, it is useful to have an indication of how efficiently plants utilize water for their growth. Water use efficiency (WUE) can be calculated in two ways (Turner & Kramer 1980):

$$mg \ CO_2/g \ H_2O$$

or

$$WUE = \frac{dry \ matter \ of \ yield}{evapotranspiration}$$

The WUE ratio can range from between 200 and 500 in humid regions to over 1000 in arid lands. In England, a crop of wheat yielding 4000 kg of dry matter per hectare and using 100–200 mm of rainfall during the growing season plus evapotranspiration from the soil will have a WUE of 500 (Fitzpatrick 1980).

These proportions are different for different plants, but it is nevertheless true that, whenever a plant is absorbing water, almost the same amount is being lost from the leaves and other aerial parts by transpiration. Yet transpiration is, in fact, the physical process upon which plants rely for the absorption of water.

The process of transpiration has been described as a necessary evil because, as plants must exchange gases with the atmosphere and as these must be dissolved before they can reach living matter, some water must inevitably escape to the atmosphere. In their evolution, the land plants have turned this imposition to advantage by adopting it to move water from the soil into themselves and thence to the air without the wasteful expenditure of energy that this would otherwise entail. Vascular plants (i.e. those with water-carrying vessels) are rather like irrigation channels diverting through themselves water that would, in any case, evaporate from soil to air. How is it done and done so effectively that even a forest giant with leaves many metres from the ground is amply supplied with water? Briefly, the process depends on the difference between the mean energy content of liquid water and that of water vapour. Liquid soil water has a higher mean energy content than water vapour, so, just as heat moves along a gradient from higher to lower temperatures, water moves along an energy gradient from media with a higher mean energy content to those with a lower mean energy content. But why through a plant?

Figure 4.6 indicates how the soil–plant–atmosphere system works. It can be seen that, because the mean energy content of water in a plant is intermediate between that in soil water and that in atmospheric water vapour, water can diffuse along the gradient from soil to air via the plant. The figures on the diagram indicate the so-called *water potential* of the water and vapour at each stage and are expressed in negative atmospheres. Water potential is the difference between the mean energy content of water at any point in a system and the mean energy content of *pure* water, measured at the same temperature. Now, if a plant is going to be efficient at transporting water across the system, it must be adapted especially to any characteristics of resistances (1) and (8), which may vary widely from place to place and from time to time according to the vagaries of climate and soil. Of course, movement of water across this system means that work is being done, and this work is a function of the proportion of incident solar radiation available to do it. The proportion varies widely geographically. In southern England in summer, about 40% of the incident solar radiation is available, while at Manaos in Brazil it is 80–90% throughout the year. At a place like
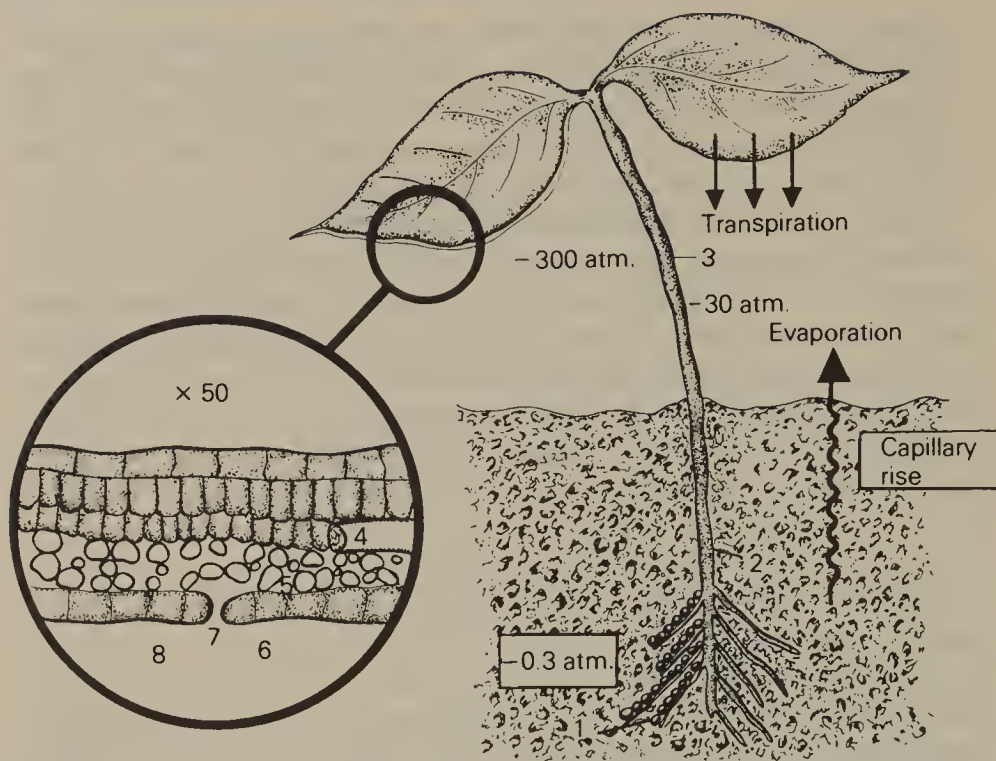
Figure 4.6   The soil–plant–atmosphere water potential gradient. Note that the figures in negative atmospheres are average examples and would be highly variable from place to place and through time (see text). The numbers 1–8 refer to the resistances which water must overcome if movement is to be maintained along the gradient: (1) soil water; (2) resistance at endodermis; (3) resistance in woody vessels (xylem); (4) resistance to passage into leaf cells; (5) resistance to entering air spaces; (6) resistance to passage through cuticle; (7) resistance to passage through stomata; (8) resistance presented by the atmosphere. Readers may find other measures of pressure used in some texts, and equivalents are given here: 1 atm = 76 cmHg at sea level (45°N or S) = 0.1013 MPa = 1.013 bar = 1.013×10^5 N m^{-2} = 1.033×10^4 kg m^{-2} = 1.013×10^5 J m^{-3}.

Aswan in Egypt, however, with little or no water to evaporate, most of the solar radiation is used to heat the air, resulting in a hot desert (Fig. 4.7).

Whether water molecules will move rapidly or slowly into the air depends very much on the resistance (8) they encounter. This depends in turn on the water potential of the atmospheric water vapour, which is determined by its vapour pressure. Vapour pressure is a function of the amount of water vapour and how much the vapour molecules are moving (i.e. their kinetic energy). The resistance encountered by water vapour in moving from plant to atmosphere will obviously be less if the vapour pressure is low, so potential **evapotranspiration** will be greater in air of lower relative humidity.
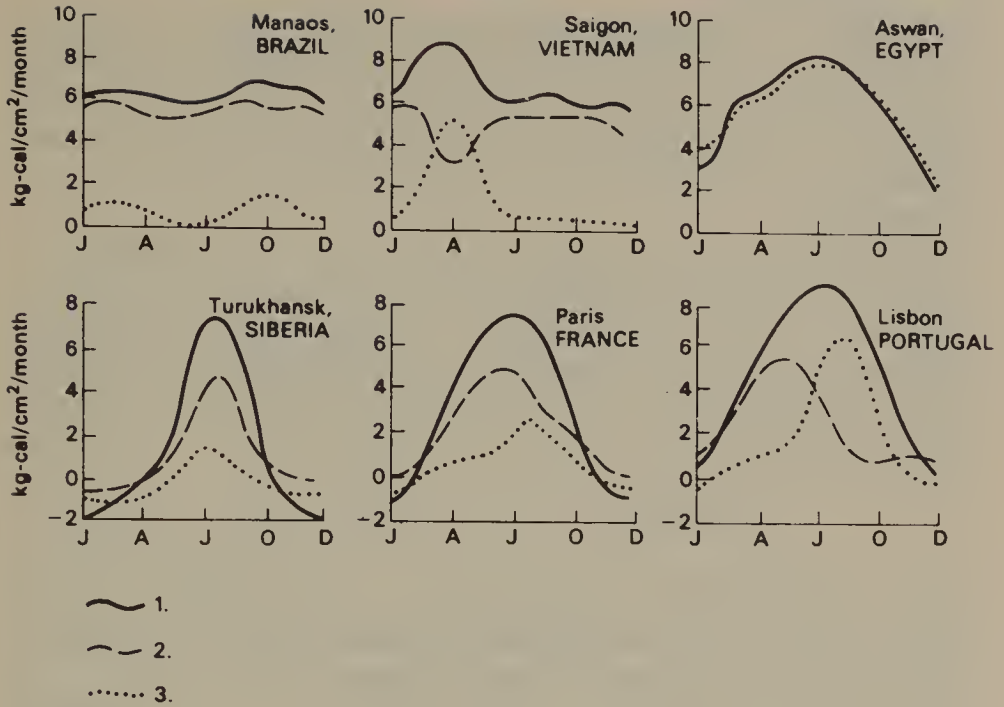
Figure 4.7 Annual regime of energy-budget components at various localities. Curves are as follows: (1) solar and infra-red radiation from the Earth and atmosphere; (2) heat transferred by evaporation or condensation; (3) heat transferred to or from the surface by condensation or turbulence. (Diagrams from Gates (1962) after data from Budyko (1958). © Harper & Row 1962.)

At 20°C, for example, air of 85% relative humidity has a water potential of approximately −220 atm, while at the same temperature air of 50% relative humidity has a water potential of nearly −1000 atm.

What happens when relative humidity is 100% and water cannot diffuse along the water potential gradient at all? Plants can, if their evolution has fitted them to, exude water as a liquid, a phenomenon known as **guttation**. Guttation seems to be a fairly widespread facility – tomato, nasturtium and many grasses are vigorous guttators when conditions are right – but it is in the trees of the hot, wet forests that it is particularly important. For example, the coco tree or taro of south India has been recorded as exuding as much as 200 ml per day from only one of its metre-long leaves. Drip-tips on these leaves may have evolved to shed the copious amounts produced by this and many other species.

In still air, diffusion of water vapour from the leaves increases the vapour content of the immediately adjacent atmosphere, raising its water potential and thus increasing resistance. Wind removes this

humidified layer and preserves the gradient. Thus in environments with abundant water and frequent low windspeeds, such as tropical rainforests (where over half the recorded windspeeds at ground level can be less than 5 mph (Watts 1955)), this problem is usually solved by guttation. In dry windy places, on the other hand, low windspeeds are beneficial.

From the practical point of view, to have some quantitative assessment of this vital habitat factor of potential evapotranspiration (PE) would be very useful. A number of workers have attempted to derive empirical formulae from meteorological data, and one that has given good correlation with the observed consumption of water by various temperate crops is that of Penman (1948):

$$E(\text{mm/day}) = 1.4 \,(1 + 0.17u) \,(e_s - e_a)$$

where u is the windspeed (in mph) at 2 m above the surface, e_s is the vapour pressure at the evaporating surface and e_a the vapour pressure at a standard distance from the source of water.

The kind of formula above requires, of course, accurate measurement at particular sites of data not normally given in climatic statistics. Other workers have had to deal with much less accurate, more generalized data in attempting to derive indices of potential evapotranspiration. It is difficult to say how valid these are. As Watts (1971) points out, 'It has not yet been proved that differences in rates of PE can be used to explain more precise changes in patterns of natural vegetation.'

On the other hand, correlations between generalized estimates of the bioclimate and vegetation can be accurate enough to be used, in some cases predictively, and in any case for practical planning purposes it is extremely useful to have some indication of climate specifically related to potential for plant growth. (See Jones (1983) for an account of plant growth and microclimate.) Indices that have been widely used are potential evapotranspiration (Thornthwaite & Mather 1956), the radiational dryness index (Budyko 1974) and the life-zone system (Holdridge 1947).

4.5   The liability of plants to moisture stress

Rainfall figures alone are a poor index to the amount of water supplied to the soil and its availability for growth. The water that is actually absorbed by the soil may be much less than rainfall figures

suggest. It is reduced by evaporation from the vegetation and surface debris and from the soil surface before it is absorbed. When the speed of infiltration is low, as in clay soils, the losses can be considerable. This accounts for the fact that in arid regions clay soils are much drier than sandy soils. Similarly, damp soils are slower to absorb water than dry soils. Thus, in well watered regions clay or humic soils have slow infiltration rates and lose more available water than sandy soils. Once absorbed, water in soil exists in four states, only some of which is available to plants, as shown in Figure 4.8.

As long ago as 1916, in a classic piece of work, Briggs and Shantz showed that a wide variety of plants could reduce the capillary water of the soil to a point where its resistance to movement became so great that its mass flow into the plant ceased and the leaves wilted. The wilting persisted until new water was added to the system. If this interval was too long, the wilting became irreversible and fatal. The amount of soil water at the point at which wilting was observed was termed the 'permanent wilting percentage' (PWP), expressed as a percentage of the dry weight of the soil. Although this might be 10% for a sandy soil and 20% for a clay soil, significantly in terms of water potential it could be the same for both, having a mean value around -15 atm and generally lying between -15 and -20 atm.

Wilting occurs in all plants in natural systems at some time or other, although it might not be visible by the drooping of stems or leaves. Physiologically it is defined as occurring whenever there is a water deficit in the plant resulting from an excess of evaporation over water absorption. Where the possibility exists that the PWP may be reached in the soil regularly, plants must have adaptations of

Imbibed water bound to clay-humus complex (not normally available to plants)

Soil water vapour in air spaces

Capillary water coating soil particles (main source of water for plants, maximum capillary water = field capacity of soil)

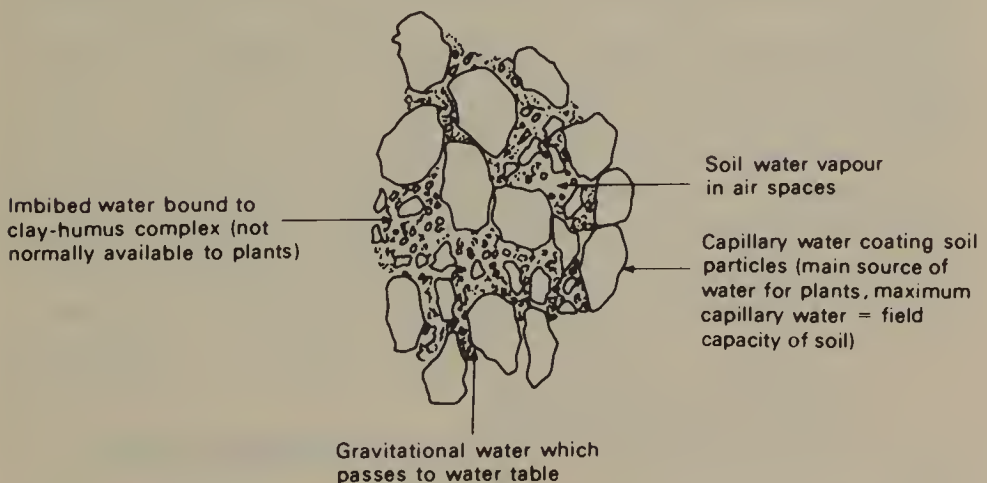Gravitational water which passes to water table

Figure 4.8   Distribution of soil water within soil particles.

morphology, physiology or life-history to enable them to survive. Whether soil moisture falls to the PWP or not is a function of soil texture and chemistry, and of climate. The latter controls the supply of moisture and the atmospheric water potential, which determine the evaporation rate. Climate also effects water uptake by its effects on soil temperature. The poleward range of many tropical and subtropical species is limited by the difficulty they experience in absorbing sufficient water at lower temperatures. Also, it is significant that many plants in the middle latitudes have strongly developed drought-resistant features even though water may be abundant during the cold season. Soil texture and chemistry control the quantity of water absorbed and retained and the way it is made available for absorption. The chemical composition of soil water – its *osmotic potential* – may, in some cases, play an important part in determining its availability. This is very true when there are high concentrations of dissolved salts as in the alkaline (solonetz) or saline (solonchak) soils. For plants to maintain a water potential gradient between the soil water and their cells, they must power their own potential by maintaining a stronger concentration of solutes in their cell sap than that which exists in the soil.

4.6   Plant categories in relation to water

There is insufficient space in this account even to begin to outline all the ways in which evolution has fitted plants to avoid the consequences of moisture stress. Most textbooks on plant physiology give good accounts and an excellent introduction will be found in Sutcliffe (1979).

Briefly, plants are conventionally classed into broad categories in relation to water supply. These are:

(a)   hydrophytes, adapted to live in open fresh water or permanently waterlogged soils;

(b)   hygrophytes, which exercise little or no control over water loss;

(c)   mesophytes, which can withstand wilting for short periods;

(d)   xerophytes, which show adaptive features of morphology, life-history or physiology, or all three, so withstanding dangerous water stress; and

(e)   halophytes, adapted to high osmotic potentials in soil water.

Although this is a useful classification, it must be admitted that

there is no absolute method of distinguishing between the five types. Plants span a broad spectrum in their adaptation to water supply, and many can withstand considerable fluctuations without permanent damage with little more than rudimentary defences against water loss. This is the case with many so-called 'mesophytes', which can adapt by changes in physiology. Also, many 'xerophytes' have transpiration rates as high as or even surpassing those of many 'mesophytes' when water is freely available. There are also unexpected anomalies in the distribution of these types. For example, many of the wet heath plants of northern Europe and tropical peat bogs are xerophytic in character yet occupy habitats with abundant water supply (Seddon 1974).

4.7   Terrestrial moisture gradients

Three moisture gradients are of importance in the evolution of geographical range in this respect:

(a)   gradients towards the centre of continents in mid-latitudes;
(b)   gradients from humid subtropical regions to the subtropical deserts on continental western margins; and
(c)   gradients from humid tropical regions to the tropical deserts, which are gradients both of increasing length of dry season and decreasing rainfall.

In south-east Asia, eastern central America, south-east Brazil and south-east Africa, although the decrease in moisture is not severe, the liability to lowered soil temperatures at certain times of the year appears effectively to limit the range of many rainforest species. This is a good example of the way in which ecological factors may act in concert. Another is represented by gradient (c) above. Experiments in West African forest reserves have shown that many rainforest hygrophyte species are, in fact, quite capable of growing beyond their normal range limit, but only when fire is excluded. They seem capable of withstanding limited drought but are intolerant of fire. The vulnerability to fire is, of course, partly a function of the vulnerability to drought.

4.8   Mineral nutrients

Table 4.1 sets out the major physiological functions and environmen-

Table 4.1 The major mineral nutrients.*

Nutrient	Physiological function	Sources	Environmental effects
Macro-nutrients			
oxygen	respiratory metabolism	photosynthesis of green plants	important determinant of plant distribution in relation to soil aeration; where soil is badly aerated or permanently waterlogged, anaerobic conditions prevent root growth in plants without special adaptations and toxic materials, e.g. H_2S, may be generated
carbon dioxide	source of carbon in photosynthesis	decay; respiration; the oceans release some 10^{12} t y^{-1}	some slight natural variations of atmospheric concentration but with little effect on plant growth and distribution; important ecological effects on soil acidity; total concentration of CO_2 (320 ppm) sets ultimate limit on photosynthesis; plants can increase photosynthesis up to 3× normal with increasing concentration
nitrogen	essential element of proteins; can only be absorbed in fixed form (NH_4, NO_2, NO_3)	drawn from the atmosphere by a host of microbes, and lightning	in most well aerated soils of intermediate acidity, fixed N usually freely available; deficiencies associated with cold, wet soils, very porous soils and tropical soils where vegetation cover is cleared; where destruction of organic matter is slow or dead material highly lignified, acid 'mor' peat may accumulate, as humification (Fig. 4.2) may be inhibited
sulphur	essential for protein synthesis and vitamin synthesis	sulphates in well aerated soils; pyrites and gypsum in arid lands; H_2S and reduced sulphur in airless soils	cycled rapidly by micro-organisms similarly to nitrogen; 'downhill' losses replaced by weathering, airborne dust, salt spray and volcanic gases; in arid regions, strong concentrations of SO_4^{2-} ions exist which select for tolerance; pollutant sources – some 146 000 000 t annually of SO_2 – increasingly added to biosphere
phosphorus	incorporated into many organic molecules; essential for metabolic energy use	Fe, Al and Ca phosphates; free anions in solution (H_2PO_4 in acid, HPO_4 in alkaline conditions)	great differences in demand between species, and hoarded tenaciously in most ecosystems; cycled on a world scale with downhill losses replaced similarly to sulphur above; oceanic reservoir returns deep-water reserve along cold currents via plankton, fish and guano of fish-eating birds (see Fig. 4.2)
calcium	essential to metabolism but not incorporated into fabric molecules of living matter	feldspars, augite, hornblende, limestone; and sulphates and phosphates in arid lands	strong selective effects in all habitats – lakes, marshes, grasslands, forests, rock outcrops; important determinant of prime physicochemical characteristics of soil; antagonistic to toxic effects of K, Mg and Na; retention of ions by colloids closely related to climate, especially rainfall
potassium	essential to many metabolic reactions, especially protein-building and transphosphorylation	feldspars, micas, clay minerals	deficiency has marked effects on carbon assimilation, thus lowering production and biomass; certain crops – beet, cotton, vine, legumes – are very sensitive

magnesium	vital constituent of chlorophyll	biotite, olivine, hornblende, augite, dolomite; and clays of the montmorillonite group	excess produces serpentine barrens, e.g. in California, Spain, New Jersey, southern Urals, Japan, New Zealand; natural climax is replaced on these by impoverished, often scrubby vegetation commonly with specialized ecotypes, e.g. *Quercus durata* in California (see Proctor 1971)

Micro-nutrients

iron	oxidation and reducing reactions in respiration	iron silicates, iron sulphates; free ions chelated with organic molecules	calcareous or alkaline soils may be deficient, as iron may be precipitated as insoluble hydroxides; may also be deficient where copper or manganese is present to excess; vines and fruit crops may be easily affected by iron deficiency
manganese	minute amounts needed for certain enzymatic reactions	ferromagnesian minerals; absorption dependent on other metallic cations	deficiencies noted in mid-latitudes especially; tropical soils, especially feralites, may have excess manganese, which has toxic effects
zinc	enzymatic metabolism	zinc-bearing vein minerals	often leached out of the soil profile in acid soils; may be insoluble in alkaline soils; certain species. e.g. *Viola calaminaria* of the Harz Mountains in Germany, are endemic to zinc-rich soils
copper	essential for respiratory metabolism	copper-bearing vein minerals	deficiency frequent in alkaline soils; any excess has strong selective effects. e.g. in Katanga, the 'copper flower'. *Haumaniastrum robertii* has 50× the normal copper content in its leaves; also *Becium homblei* cannot germinate without 50 ppm of copper at least in the soil; the latter is a reliable prospecting index for mineral veins
boron	necessary for successful cell division during growth	soluble borates are the only assimilable form	may be leached out in acid soils; some crop plants – beet, potato, cauliflower – show considerable sensitivity to any deficiency
molybdenum	essential for nitrogen fixation and assimilation	vein minerals	deficiency in acid soils frequent and also in certain tropical soils on ancient land surfaces

*The list is not complete; there are other minerals needed in minute quantities which may be involved in the metabolism of most plants or particular groups of plants. Although vein minerals may be important sources of nutrients locally, it is now clear that most non-gaseous nutrients are leached into the oceans continuously by the reaction of sea water with crustal 'hot spots' and thus most continental sedimentary rocks are contaminated with these initially. Most basaltic rocks contain the full suite of nutrients essential for growth but some granitic types may be deficient in certain micro-nutrients.

tal effects of the most important plant nutrients except water. It may be assumed that where plants are growing successfully there will be few, if any, major deficiencies of mineral nutrients, but the vegetation may well have been selected by the reactions of the plants composing it to the presence or absence of certain minerals, or to their excess or deficiency. However, there are many habitats where mineral nutrient deficiency sets severe limits to growth. Although these habitats may well have plants growing on them, the communities they constitute will be impoverished and well below the optimum production of which they are capable (Proctor 1971).

In spite of the accumulation of knowledge in relation to cultivated plants and their mineral needs since the first classic experiments by Liebig, our knowledge of the mineral needs of natural vegetation is still very poor. As we explained above, there is no natural or man-made ecosystem in which the production of the vegetation approaches the net potential photosynthesis. To what extent the gap in natural ecosystems that are not strictly limited by some other factor is due to inadequate mineral supply – perhaps only a single mineral needed in minute quantities – is not known. Certainly, the fact that agricultural systems that replace natural ones on the same site benefit from fertilizers suggests that some of the limitation may be due to this. Moreover, the discovery of the phenomenon of 'trace-element deserts' (Anderson & Underwood 1959), where production is even lower than their meagre rainfall suggests it should be, lends support to the idea that other less extreme systems may be similarly limited. Thus in one experiment in Queensland the addition of minute quantities of molybdenum increased grassland plant production dramatically (Stålfelt 1972).

Not only is knowledge of the mineral needs of true nutrients inadequate, so are the effects of those elements like aluminium, chlorine and silicon with which plants have perforce to deal. As these elements affect the soil chemistry and structure and may be absorbed and cycled in significant quantities by plants, they may divert a great deal of energy from photosynthesis which would otherwise be used for growth. (Unlike the passive uptake of water, mineral absorption is essentially an energy-using process – see Section 6.2.)

Aluminium, for example, is one of the most common soil elements and it has been shown to have marked toxic effects, especially in strongly acid soils where it is easily mobilized. In fact, there now seems to be sufficient evidence to suggest that the categories of 'calcifuge' and 'basiphilous' plants, i.e. plants that avoid or are linked to calcareous soils, contain many species that are not reacting directly

to the excess or absence of calcium but to the presence or absence of mobilized aluminium. Species that are tolerant of free aluminium appear to have some mechanism that rejects it, but what this might be is uncertain at present.

Rorison (1980, 1985) has shown in a series of elegant experiments that the effects of mobilized aluminium interact in a complex way with availability to the plant of other nutrients, especially nitrogen. Using four common British herbaceous species grown in a highly acid medium (pH 4.5), he has shown that the species (a) may be indifferent to both source of nitrogen and to variations of aluminium; (b) may be drastically affected by the form of nitrogen, thus masking any effects of aluminium; (c) may have the adverse effects of nitrogen source ameliorated by the presence of aluminium; and (d) may show no adverse effects of nitrogen source but a classic response to aluminium toxicity.

It is clear that correlations between plant distributions and mineral supply are not easily established. It is usually only under carefully controlled experiments that any firm conclusions can be suggested about the very complex relationships between plant physiology and mineral distribution. The latter is, in any case, only one aspect of the nature of soil, which in itself represents an ecosystem as complex as the one it supports, and we shall look at the relationships of the soil–plant system as a whole in Chapter 6.

In conclusion, it can be said that if mineral resources represent the 'fine tuning' of plant distribution patterns, the 'major waveband' is undoubtedly represented by water availability. Of all the materials dealt with in this chapter, it is this which supplies one of the prime keys to the understanding of vegetational geography. Wherever moisture availability is a limiting factor, the biomass of the community that can be supported, the complexity of its layering, the assemblage of its species, the growth forms they adopt and the percentage of the ground they cover are strictly governed by the availability of this essential nutrient. It is for this reason that the selective pressure exercised by water availability in plant evolution has been so powerful as to produce vegetation of similar appearance and patterns in locations widely separated geographically and composed of species belonging to genera and even families bearing little or no relation to each other. In the lowlands of the middle and lower latitudes, this factor dominates almost all the other ecological components as an explanation of vegetational biogeography.

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5

Ecosystem conditions and plant distributions

The incorporation of energy and materials into the bodies of plants composing land ecosystems takes place within a framework of circumstances that are very much conditions of place. We can list the main conditions that influence growth, but are not themselves directly incorporated into the bodies of plants, as heat, soil type, fire, wind and snow cover. Like many of the factors dealt with in the last two chapters, these conditions of plant existence have a differing impact at the species level from that at the level of the ecosystem as a whole. For example, a forest may spread continuously across large areas of the Earth's surface. However, it will be made up of different species from place to place according to the way in which the plants composing the forest respond to the different conditions they encounter. It is at the extremes of the range of an ecosystem type – forest, grassland, desert or whatever – that the conditions listed above may become important at the ecosystem level. This is especially true if, either by themselves or in combination with changing energy or materials availability, they limit the photosynthetic production needed to sustain a particular ecosystem type. This can be illustrated by the altitudinal change of vegetation on high mountains in low and middle latitudes. In these mountainous areas, there might be enough light energy and nutrients to sustain tree growth beyond the tree line. However, the lack of heat limits the ability of trees to use the energy and materials to sustain their growth and their place is taken by low shrubs and herbs. In the case of particular species, their distribution is largely *individual* within ecosystems. This is because their genetic material has been selected by evolutionary processes to respond in a particular way to the habitat conditions they encounter.

5.1   Heat, temperature and plant life

All biological processes are affected by heat conditions. Heat is a

form of vibrational energy stored in matter as the invisible random motions of the atoms and molecules of which it is composed. A measure of this state of agitation of the separate parts (their thermal energy) is its temperature, recorded by a thermometer. Heat flows from the substance – gas, liquid or solid – to the thermometer or vice versa until temperature of thermometer and substance are equal. An actual temperature, for example a degree Celsius (°C), is expressed as a fraction of the difference between two fixed and accurately reproducible temperatures, i.e. the freezing and boiling points of water at standard atmospheric pressure in this case. However, physicists may use other more precise scales than this one, based on differently defined points.

Physiological processes in plants and animals are governed in their relation to temperature by the 'van't Hoff rule' (also called the Arrhenius law). This states that a rise of temperature of 10°C usually causes a doubling or tripling of the rates of chemical reactions. This rule ceases to apply to life processes, however, once the lethal temperature of protoplasm is reached. At this point (which varies according to species but is usually between 38 and 45°C), damaging reactions become increasingly important. The thermal energy of the molecules composing living material becomes such that beyond this temperature their structure is increasingly damaged, i.e. they *denature*, and life processes can no longer continue (see Sec. 1.4).

The van't Hoff rule applies *only* to reactions directly under the control of *internal* temperatures. It does *not* apply to the variation of *external* temperatures. Thus, if the mean annual temperature of a plant habitat were to increase by 10°C, although the rates of plant metabolism might well increase, it would not produce the doubling or tripling of rates suggested by the van't Hoff rule. Plants, like animals, have means of controlling their internal temperatures. For example, in a tree, practically all the heat control is exercised by its leaves, especially through convection and transpiration, with radiation being less important. Thus, in vegetation like the tropical wet forests, where leaves are exposed to frequent high external temperatures, high incident radiation and low windspeeds, the size, spacing, albedo (reflective quality) and placing of leaves on the stem have been suggested as adaptations to energy exchange requirements dominated by the need for adequate cooling. Even the aerodynamic shape of the crown and the degree of roughness that the forest surface as a whole presents to the wind may represent a compromise between the need for adequate cooling and the avoidance of moisture stress. It has also been shown that the leaves of tropical trees have both a higher

optimum temperature for their physiological functioning – photosynthesis especially – and higher lethal temperatures (45–50°C) than leaves of temperate trees (Brunig 1971).

Where leaf temperatures are likely to be lower, as in the temperate latitudes, the problems of adaptation to the needs of temperature control are not so acute, and the leafing arrangements – branching, mosaic, whether mono-layered or multi-layered – have been more significantly related to needs other than cooling (Horn 1975). In temperate forests with dormant periods of variable length, the photosynthetic function of leaves is paramount, although they undoubtedly still serve the function of temperature regulation.

Although leaf temperatures are not wholly determined by variations in air temperatures, plant growth rates nevertheless show good correlations with external temperature variations (Gates 1968). Consequently, at a macroscale we may observe apparent correlations between plant distributions and various climatic temperature indices, such as isotherms. However, we must be very careful not to draw direct causal inferences from these. It is very tempting from the vantage point of the small-scale map to infer that species X is 'limited' by, for example, a particular average temperature in July if the isotherm for that temperature and the species distribution coincide. To determine whether the apparent correlation is *more* than a coincidence requires close observation in the field and laboratory of many more facets of a species' physiology and behaviour than the apparent response to temperature presented by map evidence.

For example, it has been demonstrated that temperature impacts differentially on plant growth processes. Thus, not all processes in plant growth are affected in the same way, and some not at all, by temperature changes in the range in which growth is possible. Waun *et al.* (1978) and Waun and Raper (1984) suggest a simple deterministic model for plant growth in relation to temperature, with five classes of parameter: (a) maximum photosynthetic rate; (b) specific respiration rate; (c) specific aging rate; (d) translocation coefficients; and (e) maximum specific growth rate. Experiments on tobacco plants have shown that (a), (b) and (c) are directly temperature-dependent, following the van't Hoff (or Arrhenius) law, but not (d), where almost complete insensitivity was shown to temperature changes in the experimental range 14–34°C. Interestingly, the specific growth rate curves obtained at the various experimental temperatures either overshot the predicted optimum growth rate at higher temperatures or undershot it at lower temperatures. No coincidence with a theoretical optimum was obtained in the experiments.

5.2   Temperature and tolerance range of plants

It can be observed in the field and laboratory that every organism has a range of tolerance of external temperature in which, during its lifetime, it can remain indefinitely active. The boundaries of this range are set by the minimum and maximum effective temperatures beyond which the organism ceases its activities and may die. Within their normal geographical range, most organisms exhibit adaptations in their life-cycle and metabolism which provide protection against these extremes during periods of growth and reproduction. Unfavourable periods of low or high temperatures may be passed as seeds or in a dormant state or by increasing the resistance of the tissues. The effectiveness of cold resistance can be quite remarkable. For example, seeds some 10 000 years old found in permafrost silt have been successfully germinated in the laboratory (Porsild *et al.* 1967).

As noted above, it is practically impossible to give a single 'optimum' temperature to which an organism is adapted. Rather, a species is adapted to a range of temperature optima for different processes, as is shown in Figure 5.1. The optimum temperature for germination, for example, may be quite different from that for photosynthesis. Although exposure to cold might seem at first sight to
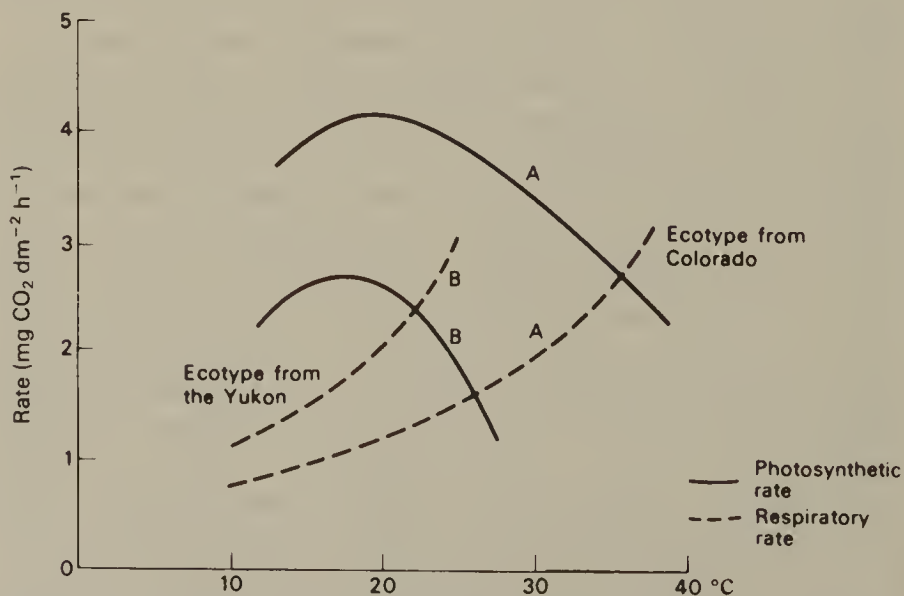
Figure 5.1   Photosynthetic and respiratory rates in two ecotypes of mountain sorrel (*Oxyria digyna*). (After Mooney and Billings (1961). © Ecological Society of America.)

be deleterious to plant growth, it has become a vital condition to ensure successful germination in some species and for the initiation of the reproductive cycle in many.

For example, temperature has an important role in stimulating germination in some buried seeds. If, for instance, a canopy gap opens, the **diurnal** soil temperature range increases, and some herbaceous seeds are very sensitive to this and germinate rapidly. The seeds of grasses, for example *Poa annua*, *Poa trivialis*, *Poa pratensis*, *Holcus lanatus* and *Deschampsia cespitosa*, in British pastures have all been shown experimentally to respond to temperature fluctuations in darkness. This capacity seems to be widespread in species composing persistent seed banks. However, very small seeds seem to require light to initiate germination (see Sec. 3.4).

Because all climates experienced by individual plants are local climates, which might vary greatly over even quite short distances, plants rarely if ever meet 'optimum' conditions in middle and high latitudes, even for only one metabolic function. Each individual plant works out its own relationship with its habitat, so that the flows of energy between itself and its surroundings are maintained by the controls on its internal chemistry and the individual adaptations of its external form.

5.3 Temperature zonation and geographical range

Four types of temperature zonation have been identified to which the geographical distributions of organisms are critically related (Hitchins 1947). These are:

(a) Control by minimum temperatures, where the limits of altitude, latitude and penetration into continents for a large number of species are set by critical minimum temperatures. In this case, a parallelism usually exists between the geographical limits of a species and the isotherms for the average temperature of the coldest month or the average monthly minimum temperatures (Fig. 5.2).

(b) Control by insufficient heat, i.e. the environment does not provide sufficient heat for the completion of at least one vital activity during the growing season. This applies particularly to the poleward and altitudinal limits of many forest species. The coincidence here would be with the isotherm for the warmest month (Fig. 5.2).
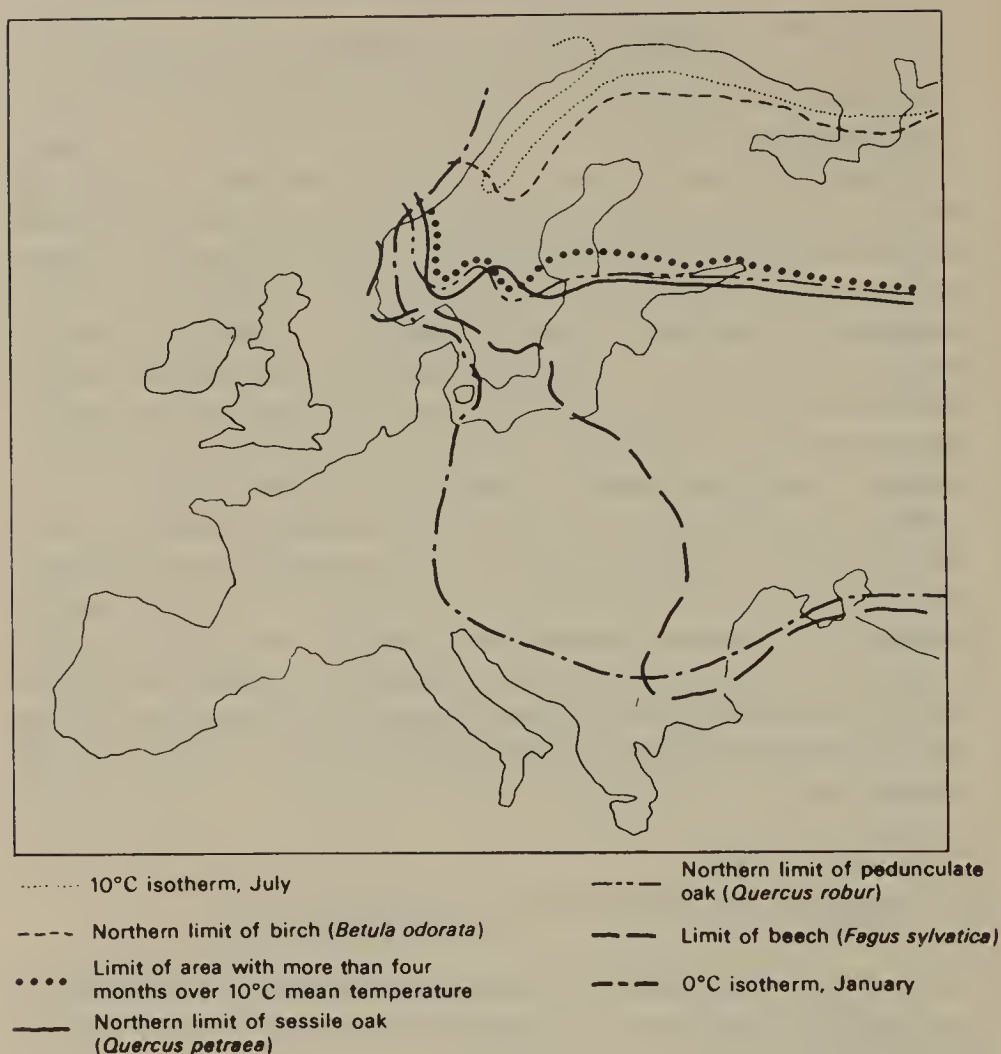
········ 10°C isotherm, July

- - - - Northern limit of birch (*Betula odorata*)

• • • • Limit of area with more than four
months over 10°C mean temperature

───── Northern limit of sessile oak
(*Quercus petraea*)

─ - - ─ Northern limit of pedunculate
oak (*Quercus robur*)

─ ─ ─ Limit of beech (*Fagus sylvatica*)

─ - ─ - 0°C isotherm, January

Figure 5.2 Relationship between average temperatures and the polewards limits of beech, birch and oak. (From various sources.)

    (c)   Limitation by excessive heat, which is a condition applying to few species directly, although one of the most important appears to be the vine, which seems to be limited by this factor in its extension eastwards from the Mediterranean (Lemée 1967). In most other species, excessive heat intervenes to limit geographical area through its effect on transpiration rates.

    (d)   Limitation due to insufficiency of temporary cold, i.e. where plants need a cold season for successful germination or the initiation of flowering. *Acer saccharum*, the sugar maple, has been cited as being limited by this factor in the southern states of the USA (Fig. 5.3).
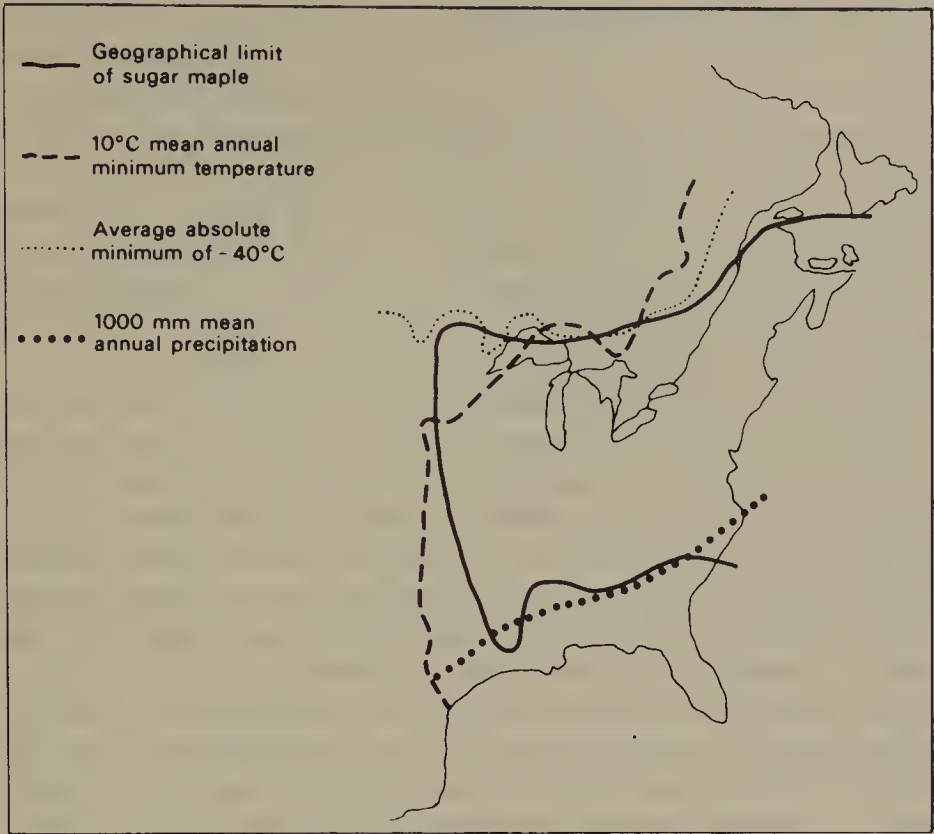
Geographical limit
of sugar maple

10°C mean annual
minimum temperature

Average absolute
minimum of -40°C

1000 mm mean
annual precipitation

Figure 5.3   Relationship of the geographical range of sugar maple (*Acer saccharum*) to various climatic indices. (After Dansereau.)

Where common thermal boundaries are shared by a large number of species, striking vegetational changes are likely to occur, as with tree lines and 'frost lines'. The latter are usually much less sharp than the former and, as is usual with most geographical boundaries, are more likely to be a zone of transition, with species being progressively eliminated across it. The striking vegetational changes inland from the Gulf Coast of North America and from southern Florida into Georgia and the Carolinas are good examples.

However, in the case of tree lines, the fall in temperature with height is not the only factor at work in many mountain areas. In Britain, for example, Pears (1968) has shown that, in the Cairngorms, the drastic reduction in height that has taken place from the *potential* tree line (600–680 m) to the present 500 m or so in recent centuries is due largely to increased wind exposure as the 'wind break' of the great Caledonian Forest was progressively removed from the 16th century onwards. Also the variation in tree lines from mountain to mountain can be seen in certain cases as a result of what has been

called the 'Massenerhebung effect', i.e. the tendency for mountain masses to modify prevailing climate significantly. This can clearly be seen in the Alps, for example, in Figure 5.4. This is not because the Central Alps are much warmer in summer than the pre-Alps. In fact, they are considerably colder at night at the heights reached by trees. Although the effect is not completely understood, it is usually attributed to the decreased cloudiness and thus the greater energy available for growth in the Central Alps. The effect can be noted in most mountain masses and is responsible for the highest levels reached by trees at 4500 m in the Tibetan Himalayas.

When we examine the polewards tree line we find also that it is rather more complicated than it appears to be on our generalized maps. Correlations are drawn between, for example, a line bounding areas of more than four months above 10°C and the northern limit of birch in Europe. In detail on the ground, however, this polewards 'limit' turns out to be not a line at all but a wide transition zone possibly hundreds of miles deep. In Alaska, there is good evidence that the polewards tree limit is not due directly to lack of summer heat at all but is much more a result of the effect of frost heaving in deeply frozen, poorly drained soil. Where good drainage exists, the white spruce can be found growing very successfully hundreds of miles beyond the accepted temperature limit. Linton (1959) notes the
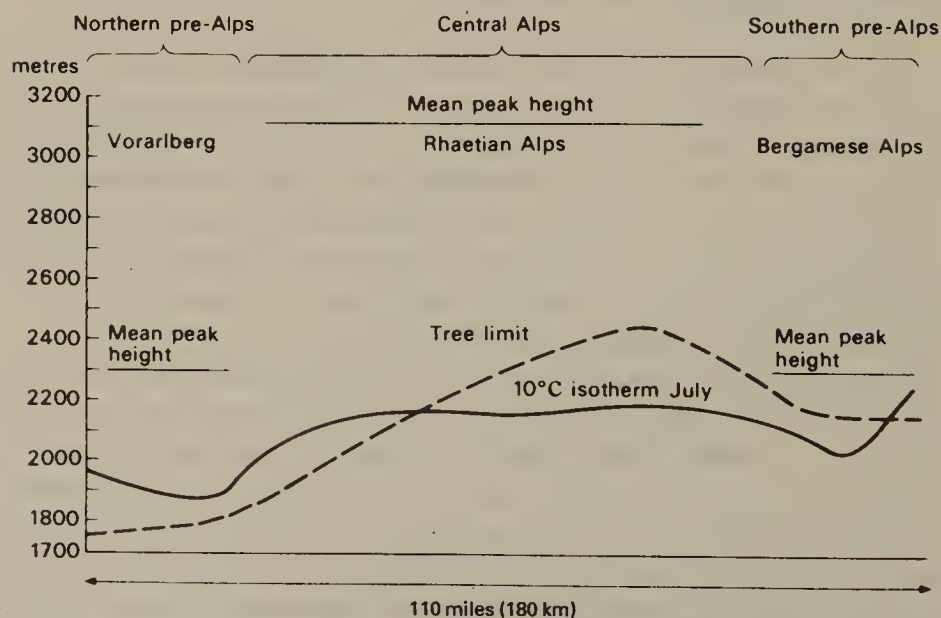

Figure 5.4   The 'Massenerhebung effect' in the Alps. (Temperature after Lemée (1967). Mean peak heights and tree limit: author.)

same scattered distribution of trees in Asia beyond what is normally taken as their limit.

In generally inhospitable thermal climatic regimes, the distributions of individual species correspond closely with those limited areas within which their thermal limits of tolerance are not exceeded. In the Northern Hemisphere middle and high latitudes, near their cold limits, plants tend to seek south-facing slopes especially on well drained soils. As winter and summer heating regimes vary in the Northern Hemisphere between slopes of south-east (warmer in summer) and south-west (warmer in winter) aspect, they may well be located in an even more intimate relationship to the details of local topography. Such is the case with the colonies of typically mediterranean plants found on some of the limestone escarpments of the Paris Basin, where species particularly sensitive to winter cold cling mainly to slopes of southwestern aspect (see Stott 1970). On the other hand, at their upper limits of thermal tolerance, species are often found on slopes facing away from the Sun or in cooler habitats like those with moist soils or forest cover. In North Africa, for example, it is possible to find many non-mediterranean species in the mountainous areas in precisely such locations. The communities may even include plants typical of the peat bogs of Northern Europe (Lemée 1967).

The very general remarks above must not be taken as being true of all species. In only a few cases are the relationships very clearly demonstrable. The box tree is one such, where it grows on north-facing slopes at the southern end of its range in Provence but on south-facing slopes at the northern end in the Jura. With the majority of plant species, however, the relationship between thermal conditions and the limit of geographical range is much less precisely seen. There may be many factors acting to prevent the further spread of a species than simply that conditions are 'too cold' or 'too warm'. This is yet another correlation too easily made, perhaps, when the facts are viewed from the vantage point of the small-scale map.

5.4   The flexibility of plant response to thermal variations

The genetics of most plant species allow them to a greater or lesser extent to vary their morphology and physiology in response not only to the differing ecological conditions encountered in their range but also to the way in which conditions may change over time in any one place. For example, the seasonal change of temperature in latitudes above the subtropics is associated with rapid, intermittent and

uneven oscillations of the Polar Front, sudden penetrations to lower latitudes of very cold air or the rapid onset of frost. Thus, the ability to withstand quick chilling and not to be caught 'napping' is one of the most important characteristics essential for survival in these latitudes. It was species possessing precisely these characteristics that survived the Quaternary glaciations in Europe and Central Asia, and still largely account for the vegetation of these regions today.

The rapid resistance to low temperatures that can be developed by some species, particularly evergreens, is striking. In the Alps, for example, at around 2000 m studies of species of heather and of pine (*Pinus cembra*) show that in mid-winter, although local minimum temperatures can fall at night to a degree or two below −20°C, it would take a fall to at least −24°C to kill the leaves of the heather and a temperature of −42°C to harm the pines. This degree of resistance is developed specifically for local winter conditions. It is not present in summer when a fall to only −4°C would kill heather leaves while *Pinus* leaves would die at −8°C. However, these temperatures are never experienced in summer, but the plants nevertheless retain a safe 'cold margin' in preparation for the first sudden temperature falls of autumn, when they quickly increase their resistance (Lemée 1967).

The intricate mosaic of habitats created by the play of temperature (and other external conditions) on the varied topography and soils of the Earth's surface may encourage genetic adaptations within species. Either ecotypes may be evolved in geographically isolated populations so that the genetic characteristics promoting survival are favoured at the expense of other characteristics (as seen in Fig. 5.1) or genetic material may be sifted into a genetic gradient. In this latter case, at any point along the gradient the species population will possess only those genes for a particular metabolic characteristic most favourable to their survival under the local habitat conditions. It is not easy, except by experiment, to demonstrate that genetic material has, in fact, been sifted out in this way. The classic method is to grow plants from different places side by side under the same conditions to see whether they retain the characteristics of morphology or physiology from their place of origin. A good example is that of Scots pine in Scandinavia. From north to south there is an easily recognizable and very close relationship between the amount of dry matter in the needles of this tree and the growth season length, i.e. number of days with a mean temperature above 6°C. When specimens were grown in the botanical gardens in Stockholm from various points along the geographical range of the plant, each maintained the amount of dry matter in the needles that would be expected from its original

location, neatly demonstrating that the gradient characteristics observed represented a true genetic gradient.

5.5   Thermal microclimates and soil conditions

The part that soil plays in determining the characteristics of thermal microclimates, although subordinate to slope angle, latitude and other factors, may be of importance in some localities, especially in their effect on seedlings. The first few millimetres above and below the soil surface (where in open sites much of the solar radiation reaches the ground) can provide an environment of extreme severity quite different from the temperature characteristics recorded by a Stevenson screen. In deserts, for example, the temperature in this narrow zone can soar in the hottest times of the year to around 65°C, i.e. well beyond the lethal temperature of protoplasm. In temperate lands, the occurrence of severe ground frosts late in spring, when seedlings are germinating, can produce critical conditions for survival.

On the whole, soils are poor conductors of heat, and in most soils daily changes of temperature are detectable only in the first 50 cm or so. Seasonal changes of temperature are detectable, however, through a depth of several metres (Geiger 1957). The kind of heating response that a soil makes to the prevailing meteorological conditions depends on its physical characteristics, especially surface colour (which determines reflectivity), mineral composition, air content and humidity. Soils of good thermal conductivity, such as damp clay soils, heat up less during the day and cool less during the night than dry sandy soils. They are also colder in spring but warmer in autumn. At depth, however, the thermal regimes of the two types are reversed and damp clays are warmer during the day and colder at night.

Where a cover of plants exists, the thermal characteristics near the soil surface are modified in many ways. Vegetation reflects more radiation than bare ground; it traps a layer of air in its branches which absorbs most of the reradiated energy; and it humidifies the air by transpiration. Consequently, diurnal temperature ranges are much modified when compared to bare ground, and the greatest are found above the surface rather than on it.

Thermal regimes are often strikingly different from one vegetation type to another. If, for example, herbs are growing thickly with leaves parallel to the ground surface, a temperature inversion is maintained between ground and leaves, i.e. the air temperature at

the ground is cooler than at the level of the leaves. Where leaves are vertical, this inversion is very near the soil surface. Under closed forests it is at the level of the tree crowns that maximum temperatures are usually recorded, with a secondary maximum at the ground surface if the leaf cover allows sufficient penetration of light. These differences induced by vegetation mean that, in describing the thermal microclimate of a wood, for example, standard screen temperatures are of very little use (see Fig. 5.5).

The gradient of soil temperature with altitude and its effect on plants have been extensively studied in recent years in north-west Europe (Green & Harding 1979, 1980, Green 1983, Tranquillini 1979). The results have shown that the effects of soil type and soil state are subsidiary to those of meteorological conditions in their effects on overall temperature conditions for plant growth except at the soil/air interface itself. Here the nature of the actual surface of the soil – its colour, reflectivity, degree of roughness and so on – may critically affect temperature conditions.

Comparison of soil temperature changes with altitude for north-west Europe and the Alps has enabled a model to be formulated that helps to explain some of the striking differences in tree lines between the two. Thus, in maritime north-west Europe, tree lines are low and irregular, with frequent scattered trees beyond the edge of closed forest. In the Alps, on the other hand, tree lines are quite sharply
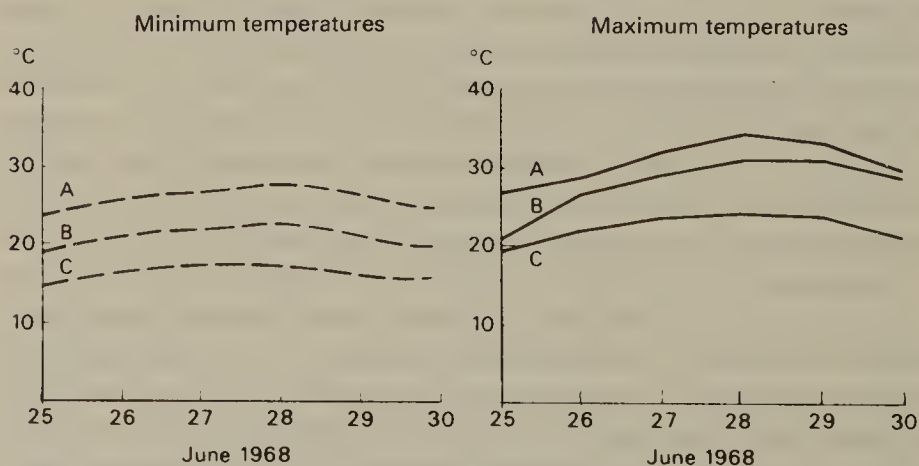

Figure 5.5 Maximum and minimum temperatures at three adjacent sites during an incursion of continental tropical air, June 1968 (screened thermometers). Curves: A, amongst tree branches (height 25 m) in closed canopy oakwood; B, under closed canopy (height 1.5 m); C, thermometer in Stevenson screen 150 m from A and B. Mean windspeed over observation period 5.8 km h^{-1} (3.6 mph). Observation site, Trent Park, Herts, England.

demarcated with few trees above, and quite close to, the tree line. The differences have been linked to two major features of soil temperature regimes in these areas. First, in the moist, cool climate of north-west Europe, soil temperatures under closed forest are cooler in summer than soil temperatures upwards from the forest edge. This may allow isolated trees to become established in locations where other factors such as wind protection and drainage are favourable. In the Alps, by contrast, the risk of 'frost desiccation' in spring beyond the edge of closed forest is much greater and prevents the establishment of seedlings. A second major difference in soil temperature regimes between the two regions is that snow cover is irregular in areas like Great Britain. This allows soil temperatures to fall to low levels between snow falls. In the Alps, snow cover with altitude is regular, and as snow cover preserves the soil temperature obtaining when it first fell, the soils are warmer in spring, having conserved heat through the winter. In other words, in north-west Europe, the differences between soil temperatures and air temperatures decreases with height in winter, whereas in the Alps, the difference increases with height. This factor may account for the fact that trees occur higher in continental mountains than on maritime uplands, an effect that can be observed directly along Norwegian fjords as trees ascend the sides inland. (Whether this is sufficient to explain all of the Massenerhebung effect mentioned above is not clear, however.)

The authors noted above also demonstrate the differential effect of vegetation height on soil temperatures; thus, the seasonal range of the temperature difference between air and soil alters approximately in a log-linear ratio to the height of the vegetation, beyond a minimum height (approximately 0.25 m). Under vegetation that is higher than this minimum, soil temperatures in summer will be cooler than those under bare ground. Cooler soil temperatures will also occur at lower altitude than under bare ground. The taller the vegetation, the lower this altitude will be. Therefore, isolated trees in north-west Europe grow in relation to soil temperatures conditioned by low vegetation. This effect is also suggested as one of the important factors conditioning the latitudinal limit of trees, which has a ragged boundary similar to the altitudinal tree line of north-west Europe.

In the USA, soil temperature regimes have been carefully studied in many environments and a generally accepted classification is widely used. The categories are: *pergelic* (permafrost), *cryic* (mean annual temperature below 8°C), *frigid* (as cryic, but with more than

5°C difference between means of summer and winter temperatures), *mesic* (mean annual soil temperatures 8–15°C plus difference between summer and winter means over 5°C), *thermic* (mean annual soil temperature 15–22°C), and *hyperthermic* (mean annual soil temperature over 22°C).

The examples given in this chapter illustrate how difficult it is to draw inferences about the relationships between plant distributions and heat energy. All such conclusions must be tentative until there is good field and laboratory evidence in support. A fact that should never be forgotten when studying biogeography is that plants and animals are *alive*. They are not inflexible machines destined always to produce the same response to the same circumstances.

5.6   Other atmospheric conditions

Wind

The global atmospheric circulation manifested locally as wind is of prime biological importance. The distribution of heat energy, the maintenance of the water cycle and the mixing of gases in the atmosphere are affected by wind. However, there are parts of the world where atmospheric movement becomes limiting to plant growth and thus has had an important role as a selective force in the evolution of species and their distribution. We can list briefly the most important effects as follows:

(a)   Strong and regular winds on sea coasts and mountains can produce distorted growth forms of various types, e.g. 'flag-form' trees, bowed trees, 'krummholz' forms (low twisted bush forms usually of conifers) and elfin forest in the tropics. 'Krummholz' can form even at relatively low altitudes, as the builders of the trans-Pennine motorway found in Yorkshire when coniferous trees planted as snow controls refused to assume a normal habit without themselves being protected from wind. Tropical elfin woodland grows at the upper forest limits and is composed of gnarled, distorted, low trees which are distinctive ecotypes of trees of normal habit found in the forest lower down. Extremely windy conditions may prevent growth altogether, as in Iceland, many of the Aleutian Islands, the Patagonian west coast, the Falkland Islands and the islands of the Southern Ocean. Significantly, some of

these locations, especially in the Southern Hemisphere, have some of the highest mean surface windspeeds recorded; between 42°S and 50°S, for example, they are above twenty knots (23 mph) in winter.

(b)   Strong, regular dry winds can increase the evaporation rate, so that in low latitudes especially plants may face extreme moisture stress. A number of workers have shown clearly the significant effect of, for example, the Harmattan wind of West Africa at both macroclimatic and microclimatic levels. In Guinea, at the headwaters of the Milo river, south-facing slopes exposed to the monsoon have over 2000 mm of rainfall per annum and are covered with dense forest, but north-facing slopes exposed to the desiccating Harmattan are savanna-covered and fires are more frequent. In Ghana, the distinctive distribution of bushes and herbs around tree clumps on the Accra plain has been related to the effects of this wind (Lawson & Jenik 1967).

(c)   In contrast to (b) above, regular humidified winds can encourage growth, as in northern California where the redwood forests are associated with frequent wind-blown fogs, or they can be limiting to tree growth as in Iceland.

(d)   The regular transport of salt spray can be limiting to coastal vegetation. In the tropical forests, for example, there is a frequently observed relationship at the coastal margins of rainforest of a low scrub composed of salt-tolerant species dividing the forest from the sea (see Fig. 18.1).

(e)   Probably the most damaging of all wind effects are those produced by the tropical cyclones. In these violent disturbances, where wind speeds may reach 150 mph, many square kilometres of forest may be flattened or badly damaged. Regular hurricane tracks affecting tropical forest may eventually produce forest sections dominated by trees at the pioneer stages of succession, and true forest climax may never be reached. Such areas of 'hurricane', 'storm' or 'cyclone' forest/scrub have been noted in the West Indies, Nigeria, north-east Australia and Malaya. Some authorities are of the opinion that hurricane incidence has been extremely important in the tropical forest in encouraging the development of new species.

All vegetation considerably modifies windspeed. Over a smooth surface such as a large lake or the sea, the decrease in windspeed is

proportional to the logarithm of the height above the surface. Over woodland or even grassland, however, the decrease in windspeed is much greater, owing to the effect of drag over an uneven surface.

Forests, particularly tropical forests which have emergent trees projecting beyond the canopy, increase turbulence markedly. This has two important effects for tree growth away from coasts and higher mountains. First, it tends to minimize the possibility of poor growth of shoots on the side of woody plants subject to frequent desiccating or cold winds. (The distorting effects of winds without turbulence on coastal or high mountain trees are usually quite clear in such locations.) Secondly, turbulence is of great importance in lowland forest in increasing convection, and therefore cooling of the canopy layer. (See Grace (1977) for a full discussion of the detailed physiological response of plants to wind.) There is also evidence that wind may be an essential factor in maintaining some vegetation types (Sprugel & Bormann 1981).

Fire

> Wherever plants grow close enough together to carry a conflagration, fire can be a significant component of the biotic environment. (Daubenmire 1978)

Even the most unlikely environments can be affected by fire. For example, the wet Tasmanian forests contain eucalyptus species, which are normally characteristic of much drier habitats. Their presence has been ascribed to fire, which need not occur more regularly than once in every 300 or 400 years to allow them to persist.

Even the wet tropical forests, which seem a most unlikely ecosystem to be affected by fire, are not immune, and extensive natural fires are reported from time to time (*Asiaweek* 1984).

If fire is a regular feature of the plant–atmosphere interaction, plants must have special adaptations to render them fire-resistant. Fire resistance is one of the most important variables in the geographical differentiation of species and in vegetational distribution, especially in the tropical and subtropical world. As fires in forests are by far the most damaging and have therefore severely tested the adaptability of trees, fire-resistant features are more conspicuous in trees than in herbs, although the less obvious adaptations of the latter may belie a considerable capability for surviving fire. Some of the kinds of adaptation to fire are shown in Figure 5.6.
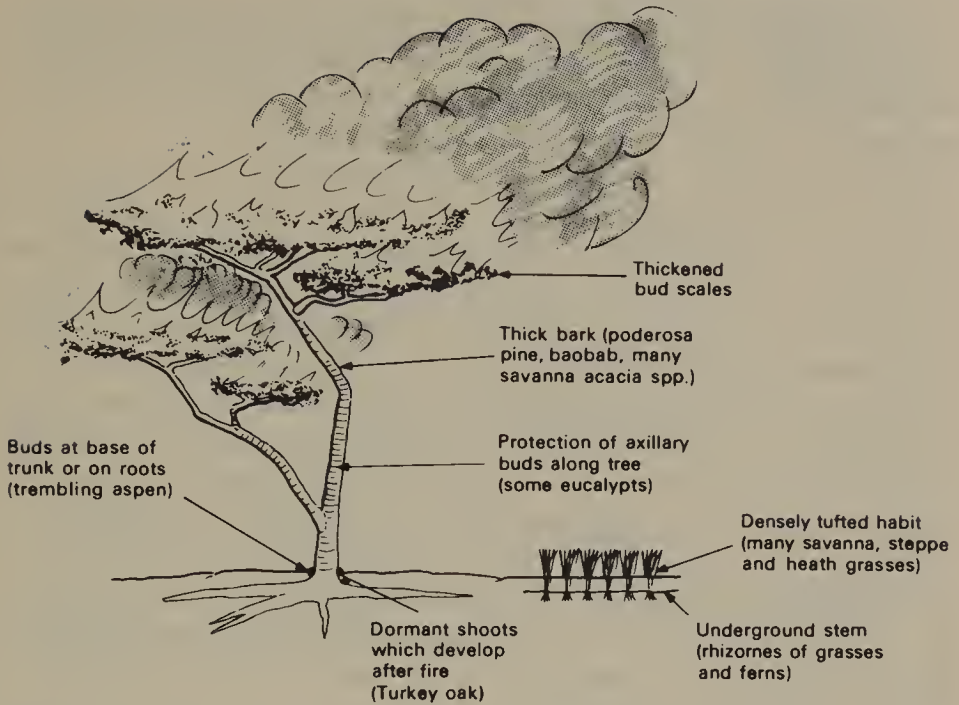
Figure 5.6   Some features of plant morphology favouring fire resistance.

Most of these adaptations are by fairly straightforward modifications of existing organs, but those that are most closely associated with fire as a selective force are probably connected with the reproductive cycle. Evidence exists that the seeds of some species are positively stimulated by fire, for example those of the valuable African forage grass, *Themeda triandra*. In the USA, the seed cones of some conifers (for example, the black spruce, *Picea mariana*) remain closed until fire-scorched while the seeds of competing species are killed.

With man's activities, fire has become so ubiquitous a condition in many parts of the world that it is almost impossible to define the nature of the true vegetation type. In Australia, for example, the eastern Australian forests contain a full range of resistance from very fire-sensitive to completely fire-tolerant species. These have been sifted by fire (either natural or man-induced) into protection-dependent and fire-tolerant vegetation types. North of 32°S where fires are of the surface variety (i.e. they do not burn from crown to crown), the frontier between the two vegetation types tends to oscillate between eucalypt-dominated, fire-tolerant forests and fire-sheltered raingreen or rainforest types, the border shifting with the impact of fire. In the south-east of the continent, fires are mainly of

the very destructive running-crown type with mass ignition. These are extraordinarily violent, with whole stands of trees practically bursting into flame simultaneously. They are so destructive that it is practically impossible to define the true climax vegetation.

The frequency of natural and man-induced fires in the world's grasslands also introduces an element of doubt into the definition of their 'natural' state. There is certainly good evidence that, given fire protection, in many of them grassy vegetation can be rapidly superseded by trees, for example by the building of roads as in the Upper Mississippi Basin (Daubenmire 1978) or by the presence of rivers opposed to the direction of the prevailing wind. The last case is well shown in the Llanos of Colombia where the rivers running east-west interrupt fires driven by the prevailing northeasterly winds, and woodland grows on their southern banks (Blydenstein 1967).

However, Axelrod (1985) has shown that fire in the grasslands of North America is integral to the maintenance of vegetation type. It has also been pointed out that it is the essential factor maintaining the vegetation in other ecosystems, for example some conifer forests (Heinselman 1971, Foster 1985).

The controlled use of fire seems to have been achieved around 500000 years ago. From that time there is evidence that Palaeolithic man was well aware of its efficacy as a hunting technique. In Spain, for example, at Ambrona around 300000 years ago, a herd of 40–50 short-tusked elephants were driven by fire into a swamp and there efficiently butchered. Such use of fire must certainly have had ecological effects. As to how widespread these were it is difficult to say. However, fire driving as a hunting technique can be traced practically down to the present day (Daubenmire 1978, Sauer 1971).

From 11000 years ago the first agriculture appears in the record, and it is now clear that it developed in a number of widely scattered places around the world – the Near East, Meso-America, Peru, the Yangste valley and interior Thailand – within a span of 6000 years or so (Bender 1976). Wherever it developed, fire seems to have been involved as an integral agriculture technique and remains so in many parts of the tropical world to the present day. 'Slash and burn', shifting cultivation and 'swidden' farming all employ burning as (a) a quick method of land clearance, and (b) a means of unlocking nutrients from dead plant material. Whether it will actually increase yields depends very much on climate. If conditions are too dry, much of the nutrient material in the ash may be blown away. Where rainfall is abundant and reliable, however, the increase of yield can be spectacular (as much as 100% in some experiments in the USA). On

Absolute age B.P.	Technological innovations	Archaeological designation	Glacial and *Inter-glacial* sequence in Alps and Great Britain
1	Fossil fuel		
2	Water power		
3		Iron Age	
4			
5	Wind power		
6	Metal working Irrigation	Bronze Age	
7			
8	Towns (e.g. Jericho 2–3000 pop.)		*Flandrian*
9	Pottery		
10,000	Agriculture and villages	Neolithic	
50,000	in Near East Blade tools e.g. Aurignacian	Meso-lithic / Middle and Upper Palaeo-lithic	Main Wurm (Devensian) (1)
150,000		lithic	Early Wurm / *Ipswichian* (2) / Riss II (3)
250,000	Hand axe (Acheulian) / Flake tools (e.g. Clactonian)	Lower Palaeolithic	Riss I (Gipping) (4) / *Hoxnian* Late (5) / Mindel (Anglian) (6)
350,000			*Clactonian* Early Mindel Cromerian (7)
450,000			Late Gunz (8)
550,000	Fire control		Gunz II / Gunz I
	Pebble tools e.g. Olduwan		

(Left margin dating labels: ¹⁴C dating; Approximately 440 human generations; UNRELIABLE DATING; Dating by ⁴⁰K – ⁴⁰Ar)

Possible American equivalents: (1) – Wisconsinan (2) – *Sangamon*; (3) Illinoian (?); (4) – Illinoian (?); (5) – *Yarmouthian* (?); (6) – Kansan (?); (7) – Aftonian; (8) – Nebraskan (?)

Figure 5.7 Stages of recent human cultural evolution. (Data from Bender (1976), Goodall (1975), Fleming (1976) and West (1968).)

the other hand, if burning is done too frequently, the nutrient reserve begins to fall and yields decline. In Africa, the frequency of burning is closely related to population pressure. As population rises, the intervals between burning decrease, and with them the ability of the soil to recover after farming.

This point illustrates what is now one of the most important

conditions for the operation of ecosystems around the world and the soils that sustain them. There are very few parts of the world now where man is not one of the dominant influences in the life of the land plants. During the long period of **Palaeolithic** culture before 11000 years ago man the hunter–gatherer was limited in population by what could be obtained from the wild in the leanest season. At their maximum, there were probably no more than 20 or 30 million human beings around the world. With the invention of agriculture, world population has steadily increased to its present 4000 million plus, and the clearance of land to sustain the human population has by no means finished. In China, the USSR, Brazil and India and on the African continent the process of land colonization is still rapidly expanding. As to how rapid this process has been, Barbara Bender has provided a telling analogy. If we compare the total span of human life on Earth to a period of 18 days, the hand axe was invented two days ago, fire control yesterday and everything from agriculture to the moon-shots has occurred in the *last half-hour*. Figure 5.7 sets out the timescale of these later changes diagrammatically, and in Parts 2 and 3 of this book we shall look more closely at some of man's effects on the vegetation of some of the world's major ecosystem types. (See Koslowski and Ahlgren (1974) for a fuller discussion of many of the effects of fire in the world's ecosystems.)

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6

Soil conditions and their influence on plant distributions

As a habitat factor, the influence that soil has on plant growth is profound. The soil itself is a system as intricate as the vegetation it supports. Even to outline the numerous geographical, geological, climatic and ecological relationships between the atmosphere, plants and soils would be outside the scope of this book; good accounts will be found in Eyre (1968) and Watts (1971). However, the basic principles of the relationships can be expressed relatively simply in the form of a schematic systems diagram (Fig. 6.1).

6.1   The atmosphere – plant – soil system

Figure 6.1 shows that the limiting boundary of the system is set by the energy and atmospheric conditions, which affect (a) the nature of both plants and soil directly, and (b) the connecting processes between the two contained systems. This figure also indicates the critical importance of the root/soil interface (*rhizosphere*), which forms the direct link between the two systems. It is the response of the root to the soil that determines whether plants become established in an area. Figures 6.2 and 6.3 show that the root/soil interface is a much more complex thing than we might think. In the near-root zone, for example, there is always a vast population of micro-organisms positively associated with the higher plant and dependent on the exudation of food from its root. This penumbra of microbes has an important role to play in return for its energy supply. They can exude enzymes (organic catalysts) that break down normally insoluble minerals (e.g. calcium triphosphate) and they protect the plant from attack by other harmful microbes and fungi. The fungi that infest the roots of practically all higher plants – termed *mycorrhizal*
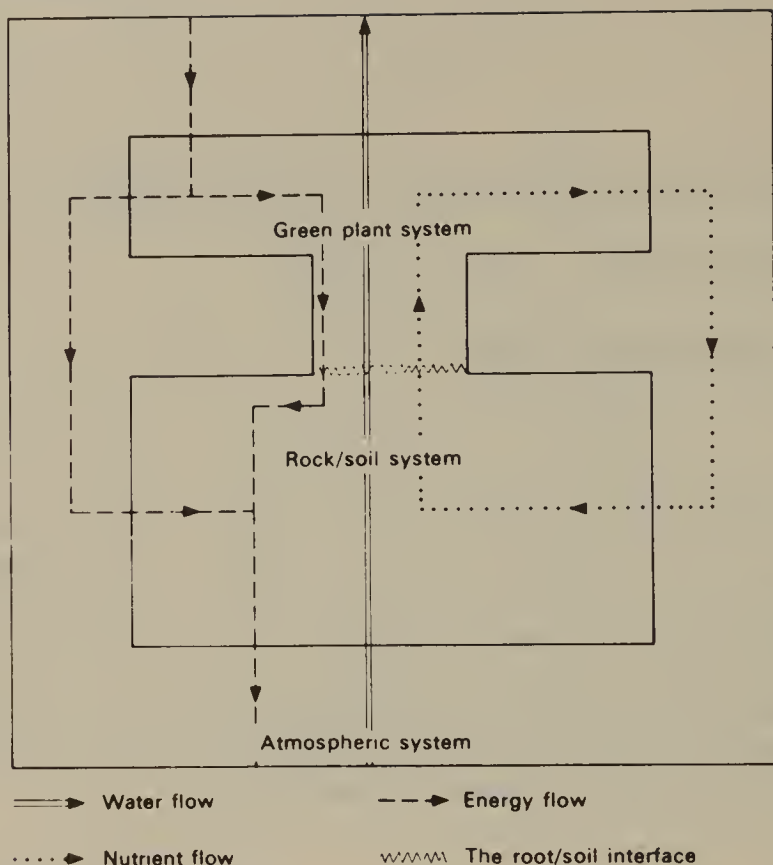
Figure 6.1   Schematic systems diagram of the atmosphere–plant–soil system.

fungi – are of two types, endotrophic and ectotrophic. The latter, which spread into the soil, are extremely important in maintaining the mineral nutrition of the herbs and trees with which they are associated. They form an enormous surface area for absorption, and feed into the higher plant mineral salts and possibly water also (see Sec. 4.1).

The successful establishment of a green plant essentially depends on whether and in what form the soil can supply the root with water and mineral salts. As we saw in Chapter 4, the movement of water is largely outside the control of the plant, but that is not entirely so in the case of minerals. Figure 6.2 indicates that the two flows of water and mineral salts are different. The former process is passive and dependent on the physical state of the soil – plant – atmospheric water potential gradient, but the flow of minerals is an energy-using process; the plant has to do some work for its food.

Although the process is by no means fully understood, a model of how plants obtain their mineral nutrients from the soil is now widely
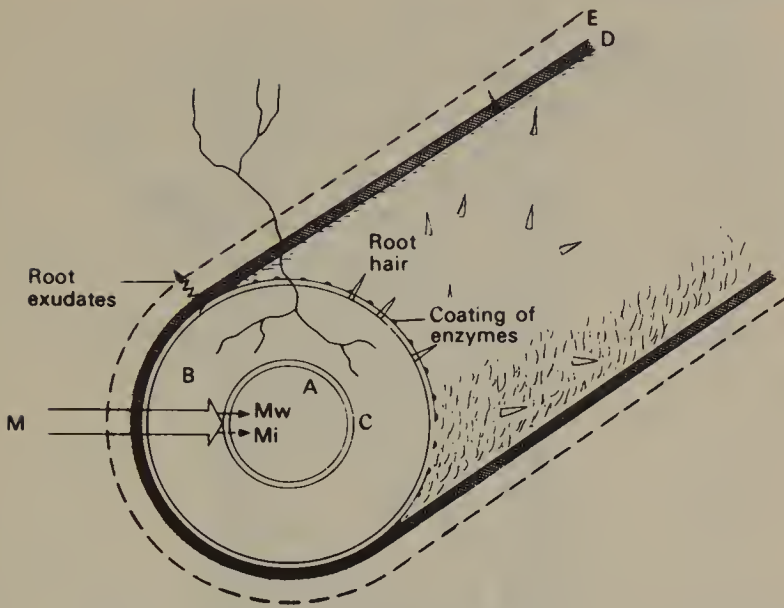
Figure 6.2 Schematic diagram of young root/soil interface: A, stele; B, cortex; C, endodermis; D, near-root zone of electrical neutrality; E, zone densely populated by micro-organisms. Processes: M, transport of water and ions; Mw, transport of water; Mi, ion transport by carrier compounds across endodermis.

accepted. The elements needed for nutrition are absorbed by the plant in the form of charged particles or *ions*. Metal ions and hydrogen are positively charged (cations) and non-metals are negatively charged (anions). In soil solution, the concentration of free ions is usually low, as most of the cations and some of the anions, phosphorus especially, are bound to the clay and organic fraction of the soil. Of the major mineral nutrients, only nitrate and sulphate ions occur mainly as free ions in soil solution. Anions are absorbed by higher plants almost wholly from the soil solution. Cations can be obtained from the soil solution but also by direct exchange between the root and the soil particles in some acid conditions. In this case, CO_2 diffusing from the root reacts with soil water to produce carbonic acid. Hydrogen from the carbonic acid displaces cations from the clay and organic particles, and the cations are thus free to be absorbed by the root.

Transport to the root surface of cations and anions takes place both by mass flow, as water is absorbed, and by diffusion. As ions are moved to the root and absorbed, their concentration in the immediate soil water will be lowered, so more ions may be released to soil water from the soil particles. Thus, the absorbing root, soil water and soil particles will be in a state of dynamic balance, which will be maintained as long as the root is absorbing water.
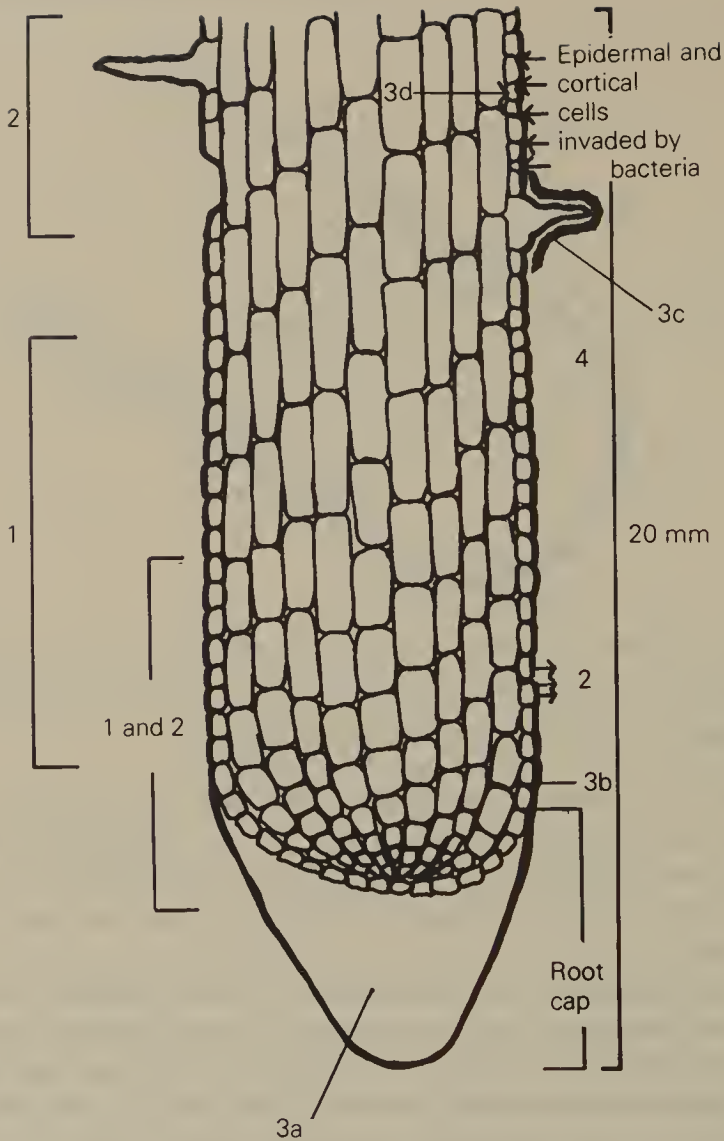
Figure 6.3 Origin and nomenclature of the organic materials in the root-tip rhizosphere. (1) Exudates into the rhizosphere by leakage. (2) Secretions of low molecular weight compounds and high molecular weight mucilages released as a result of metabolic activity. (3) Plant mucilages: (a) mucilages originating in the root cap and secreted by the Golgi; (b) hydrolysates of the polysaccharides of the primary cell walls between sloughed root cap cells and epidermal cells; (c) mucilages secreted by epidermal and root hair cells with only primary walls; (d) mucilages produced by degradation of the primary cell walls of old epidermal cells. (4) Mucigel produced by root–soil microbial complex. This maintains contact between root and soil as root shrinks during daytime hours and permits continuous intake of water and mineral salts. (After Rovira *et al.* (1979).)

The penumbra of microbes and fungi that surround the root (called the *rhizosphere*) also influences the uptake of ions. Some of the rhizospheric flora divert ions for their own needs but others positively aid the higher plant. For example, some bacteria are capable of exuding enzymes that can liberate phosphorus from phosphatic minerals, and the ectotrophic mycorrhizal fungi are important in enhancing the capability of the plant to accumulate particular nutrients such as nitrogen in temperate acid soils (see Sec. 4.1).

The root epidermis can be shown by simple experiment to provide no barrier to the entry of charged particles. Once within the root, the ions cross the cortex to the endodermis via two pathways. The first is that provided by the fluid occupying the free space within the structure of the cell walls of the cortex. (Estimates suggest that at least 10% of the cell walls are free space; this is called the *apoplast*.) Experimental evidence suggests that this fluid is continuous with the soil solution as far as the endodermis. In an absorbing root, the mass flow across the free space in response to the water potential gradient created by the transpiration flow carries ions with it to the endodermis. They may also diffuse through the free space medium.

The second route is represented by the cell cytoplasm. As the cell wall free space contains fluid continuous with that of the external soil, the outer membrane of the cytoplast (the *plasmalemma*) is in direct contact with this fluid and ions may be absorbed from it by the cortical cells. Thus, the cortical cell membranes represent an enormous surface area for the absorption of ions, although there is some uncertainty as to the details of how this absorption takes place. Unlike animal cells, the cytoplasts of individual plant cells are intimately connected by cytoplasmic threads (*plasmodesmata*) to their neighbours, and the whole network of cytoplasts and threads is called the *symplast*. It is via this unified symplastic network that absorbed ions are moved inwards to the stele. The details are not fully known, but evidence suggests that diffusion through the watery phase of the cytoplasm, attachment of ions to protein carriers within it, containment of ions in small vesicles and direct protoplasmic streaming from cell to cell may all play a part.

Ions may also cross the inner membrane of the cells (the *tonoplast*) and be accumulated in the cell vacuole. Useful ions usually reach the stele and are transported away from the root; others that are excess to need may be stored to maintain the cell sap concentration or expelled from the root altogether back to the soil solution. Most of the useful ions absorbed are transported eventually to the shoot and distributed according to metabolic need. Within the plant, the

mobility of the different elements varies widely. Phosphorus, for example, is highly mobile, but calcium usually remains at the site of its initial deposition from the transpiration stream (Sutcliffe & Baker 1981).

The endodermis (Fig. 6.2) provides a limit to the free space of the root. This cylinder of cells has strips of fatty material (suberin) deposited on the radial and tangential walls of the cells, which ensures that water cannot move passively via the apoplast from stele to cortex and vice versa. It can only move through the endodermis via osmosis. Ions and sugars, etc., can move inwards or outwards via the symplastic route. It has long been known that the uptake of ions is an active rather than a passive process, requiring the expenditure of metabolic energy. Food as well as favourable temperatures and aeration are necessary for successful mineral nutrition. For example, most well drained soils are sufficiently aerated and roots can obtain oxygen quite easily, but in waterlogged or compacted soil this is not the case. This has been an important selective factor in the evolution of some species, for example the plants of mangrove swamps. Here specialized breathing organs (*pneumatophores*) have developed, which project above the mud or low tide, allowing free oxygen exchange. Less extreme examples are the alders and willows of wet temperate sites, whose woody tissues contain sufficient air spaces to allow diffusion from above ground.

A further sign of the 'active' nature of mineral nutrition in plants is the selectivity displayed by many species. It is fairly certain that plants absorb in greater or lesser amounts every element presented to their roots by the environment. (It is for this reason that polluting elements such as plutonium can so easily enter the food chain.) However, before an adequate model was available for the mechanisms of mineral nutrition, it was known from experiments that excess of particular minerals supplied to plants resulted in a decline of other minerals in the ash content of plants. Thus, at Rothamstead Experimental Station in Hertfordshire, England, potassium applied to grass as a fertilizer increased its proportion in the ash content and lessened the proportions of sodium, calcium and phosphorus. It is now realized that, because mineral absorption is an active process, probably involving carrier molecules, there is 'competition' for attachment sites on these molecules. An excess of one mineral can therefore produce a deficiency in supply of other minerals as the preponderant element occupies a disproportionate share of the carrier system. Thus, in limestone soils, for example, with high calcium levels, there will be a reduction in the levels of potassium and

sodium. Phosphorus and magnesium may also be deficient. High levels of calcium are usually also associated with marked alkalinity in the soil, and this, in itself, makes iron and manganese hard to obtain, as they are converted from readily absorbed ferrous (Fe^{2+}) and manganous (Mn^{2+}) to less easily absorbed ferric (Fe^{3+}) and manganic (Mn^{3+}) forms.

The active nature of mineral nutrition also allows plants (which evolution has adapted to do so) to reject otherwise harmful elements. Thus plants of acid soils where aluminium is mobilized appear able to avoid its absorption. However, some plants, for example species of club-mosses (*Lycopodium* spp.) and species of the angiosperm family *Diapensiaceae*, accumulate large amounts of this element. Amongst terrestrial halophytic plants, sodium is accumulated in excess of potassium, whereas in marine algae the reverse is the case, although in sea water potassium is present in lower concentration than sodium.

These processes of mineral absorption have exercised a strong influence on terrestrial plant evolution.

If, from germination onwards, a plant has difficulty in establishing its relationship with the ionic content of soil water, or cannot encourage fungi to infect its roots, it will be at a considerable disadvantage in establishing its seedlings, which may have to compete with the seedlings of many other species. As soils vary widely in their chemical nature, the evolutionary process has ensured that this selective force has had an appropriate response in plant genetic material, so that many species, ecotypes or varieties of species are adapted with great efficiency to the establishment of their seedlings in particular kinds of soils (Fig. 6.4). Even where different species are growing successfully in the same kind of soil, they will nevertheless have a differing relationship to the soil mineral salt content. This can clearly be shown by the differing proportions of elements in the ash content of the plants. That these proportions of ash elements are genetically determined was demonstrated by Weiss (1943). Here two varieties of soya bean (*Glycia max*) grown in the same medium took up iron in different proportions. This was shown to be the result of a single gene difference. In most plants it is probable that differential abilities in mineral salt absorption are controlled by several genes. Once taken up by plants, useful elements are held onto tenaciously, especially those which are highly mobile. In a famous experiment using isotopic forms of various minerals, Bukovac and Wittwer (1957) demonstrated a gradation of mobility in elements from those which are highly mobile (Na, K, Mg, P, Cl, S) through those which are partially mobile (Zn, B, Mn, Fe, Mo) to those which are
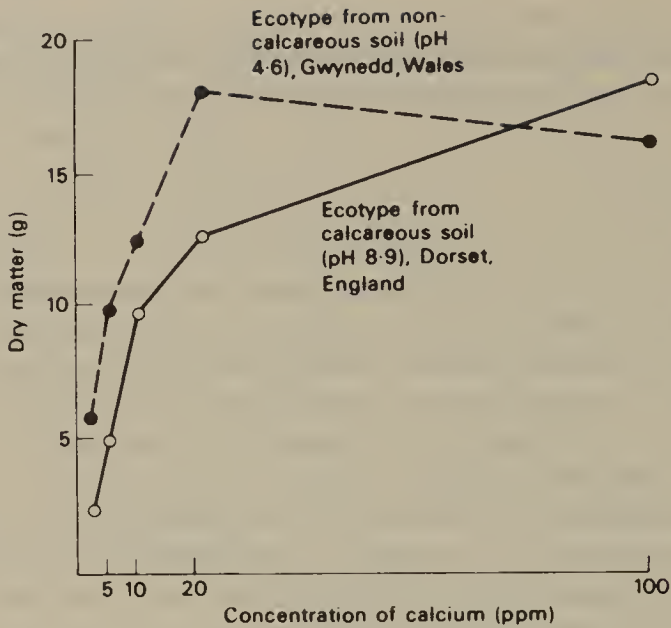
Figure 6.4 Growth of two ecotypes of sheep's fescue (*Festuca ovina*) in varying concentrations of calcium. (After Snaydon and Bradshaw.)

practically immobile (Ca, Si). When plants shed leaves, most of the mobile elements are withdrawn, leaving especially calcium, boron, manganese and silicon. The internal mobility of some elements can be astonishing. Thus Biddulph (1959) demonstrated that a given phosphorus atom can make several complete circuits of a small herbaceous plant in 24 h.

The actual quantities of elements shed in plant litterfall varies from species to species and from one vegetation type to another (Fig. 4.5). This has major consequences for those components of an ecosystem dependent on litter for their food. It is also important in its effects on the soil structure and chemistry. In temperate lands, there is a well known distinction between leaf litter that is relatively rich in ash elements and low in acids ('mull' or mild humus) and leaf litter that is low in nutrients and high in acids ('mor' or acid humus). The former would be exemplified by the leaf litter of lime, (*Tilia* spp.), ash (*Fraxinus* spp.), holly (*Ilex* spp.), elm (*Ulmus* spp.) and oak (*Quercus* spp.), the latter by beech (*Fagus* spp.), *Vaccinium* spp., *Erica* spp. and many conifers. (The processes by which the elements are returned to the soil are dealt with in Section 4.1.)

6.2 The ionic state of soil water and plant behaviour

The supply of mineral nutrients to plants depends on their presence

in solution in soil water. Fortunately for all living things, water, in spite of its ubiquity, is a very unusual substance. It tends to dissolve a great many materials relatively easily, and once dissolved they tend to stay dissolved. This property stems from what is called the *dielectric constant* of water. This is a measure of how well the medium keeps oppositely charged particles apart. The dielectric constant of water is greater than that of almost any other medium. Thus, apart from water vapour, which is always pure, and ice, which is sometimes pure, water in nature is never pure. It is always contaminated by a mixture of positively and negatively charged particles. The measure commonly used to obtain some idea of the ionic state of soil water is that of pH. The pH number is a measure of the concentration of free hydrogen ions (H^+) and is the logarithm to the base 10 of the degree of dilution. This means that if 1g of a litre of soil water is one hundred thousandths by weight hydrogen ions (i.e. $1/10^5$ or 10^{-5}), its pH is said to be 5. Pure water, which has both free hydrogen ions and hydroxyl ions (OH^-) balanced equally, or neutral solutions, have a pH of 7. That is, they contain 10^{-7}g of H^+ per litre. Acid solutions have more hydrogen ions and thus numbers less than 7; alkaline solutions have numbers greater than 7. Conventionally, the range can be from 0 to 14 but most soils lie between 3 and 10 and marine environments between 8 and 9.

The pH number can also tell us something indirectly about other elements in the soil. Hydrogen is a very active element. Within the soil water, if it comes into contact with a negative charge (or **valency**), it will hook itself on very quickly. The most likely source of these 'hooks' are the negative valencies not already occupied in the material (clays and humus) in the soil. In fact, the clay–humus **colloids** show a 'preference' for attachment of positively charged particles taking them up in the order $H>Ca>Mg>K>NH_4>Na$. Now, if there are a large number of free hydrogen ions in the soil water, we can conclude that pretty well all the negative valencies of the clay–humus colloids will be saturated with hydrogen and the other positively charged ions will be free in the soil. This would be the case with a pH of 4 or below. If, on the other hand, the pH is greater than 8, there will be fewer free hydrogen ions. We can infer one more thing of importance from the pH of soil water. When the number is low, 4.5 or less, and the positive ions are free, they are very liable to be **leached** out by any water draining down through the soil. It is no accident that soils poor in bases are especially those with low pH numbers. Of course, the pH cannot tell us anything about the exact amounts of bases available to plants or about their proportions.

Other more complex methods must be used to obtain these figures.

Rorison (1980) has listed the effects of adverse pH conditions as follows:

(1)   the direct effect of hydrogen ions themselves, which can attack delicate cell membranes;

(2)   the effect due to low pH on

    (a)   the physiological ability to absorb calcium, magnesium and phosphorus,

    (b)   the increased solubility and therefore toxicity of aluminium, manganese, iron and other metals,

    (c)   the reduced ability for aluminium and phosphorus interactions and

    (d)   the reduced availability of molybdenum;

(3)   the low base status of soils, which results in

    (a)   calcium deficiency and

    (b)   deficiencies of magnesium, potassium (and possibly sodium) especially;

(4)   the creation of abnormal biotic conditions, resulting in

    (a)   impaired nitrogen fixation and cycling,

    (b)   impaired mycorrhizal activity and

    (c)   the possibility of increased attack by soil pathogens;

(5)   the accumulation of soil organic acids or other toxic compounds due to unfavourable oxidation–reduction conditions.

Given such a comprehensive list of adverse effects it is hardly surprising that significant correlations should exist between the distribution of many species and soil pH. It has also been noted that the effects are most apparent in the seedling stage, when plants are establishing their roots. Thus, if a fully grown mixed ley grass pasture is limed (i.e. made more alkaline) almost nothing happens, but if it is limed *before being seeded* the effects on its composition are dramatic and result in what is to all intents and purposes a monoculture. Grasses not suited to a more alkaline pH as seedlings do not become established.

If we try to find out in the laboratory why some seedlings do better than others in their reactions to the pH of the first few millimetres of the soil surface, a very odd thing happens. Given the same range of
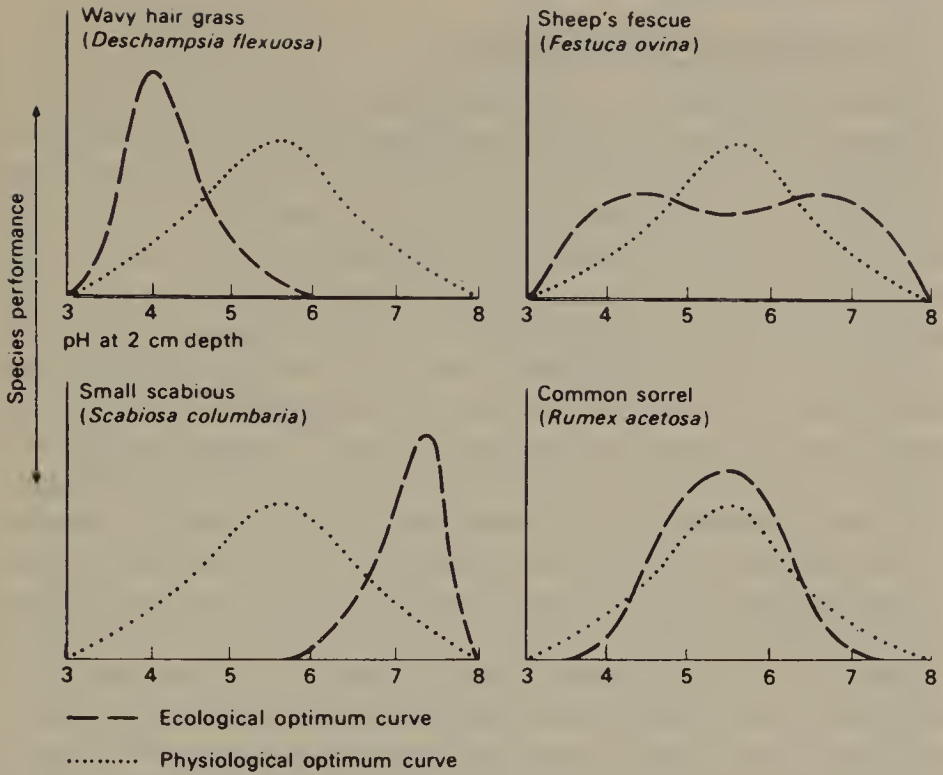
Figure 6.5 'Ecological behaviour' and 'physiological behaviour' of four competing species in establishing pastures in the Sheffield area. The ecological optimum curves were established from the relative frequency of each species in 340 m² random sample plots in acid pastures. The physiological optimum curves were established for each species from observation of their growth performance under non-competitive conditions in controlled laboratory plots. (From Rorison 1969.)

pH conditions, species often tend to perform equally well. Figure 6.5 shows this very clearly in four species taken from acid soils in the Sheffield area. However, under *competitive* conditions they perform quite differently, as can be seen.

Thus, we must distinguish between 'physiological behaviour', which we can measure in a laboratory, and 'ecological behaviour', which is the way the plant actually behaves in nature. This distinction applies not only to the way plants respond to pH but to many other ecological factors as well. It can be observed that the ecological behaviour in many species, especially near the limits of their geographical range, may be far removed from any physiological optima for them obtained in the laboratory in relation to heat, light, water supply, mineral nutrition and so on.

6.3   The effects of plants on soils

The main effects that plants have directly on soils – as opposed to the indirect effects they produce by modifying insolation, wind, temperature and other climatic elements – is the way in which, once established, they almost literally 'mould' a home for themselves by altering the soil to suit their needs. This is achieved in a number of ways, but especially by the litter that plants shed. First, the organic compounds in the litter represent the energy supply for soil fungi, mesofauna and macrofauna. Cut off this energy and the soil rapidly changes its character as it ceases to be churned and burrowed into by the animal populations. It may become compact and airless and liable to erosion. Secondly, litter supplies the vital humus that sustains the **clay–humus complex** and contains the reserves of soluble nutrients. The nature of the humus in turn is dependent on its processing by soil organisms (see Fig. 4.4). Thus a leaf litter low in organic acids and rich in nutrients will encourage a high population of soil organisms and produce a mild humus, while one that is low in nutrients will produce an acid humus. In southern British woodlands, for example, within quite short distances on broadly similar mineral substrates, soil can change character dramatically according to the superjacent tree species. On gravel soils in the Hampshire New Forest, it is possible to find rich, well drained, mildly acid soils with a rich meso- and macrofauna under oak and holly only a stone's throw from shallow, leached acid soils (podsols) with low soil faunal populations. Chalk soils near Eastbourne in Sussex provide an extreme example. Here Scots pine (*Pinus sylvestris*) plantations originally planted in shallow limy rendzina-type soils are now underlain by leached brown forest soils, which in some cases have become podsolized. It has also been demonstrated that, once the acid litter is removed as a result of tree-felling, the process can be reversed. Dimbleby (1952) has also shown that the shallow, leached podsolized soils of acid moorland in north-east Yorkshire can be converted to deeper, brown forest soils over time by the planting of broad-leaved oak and ash forest.

Leaf litter affects the soil chemistry directly by means of the organic compounds it contains. Leaves with abundant organic acids or strongly lignified tissues are not easily eaten by the soil fauna and tend to decompose slowly by wetting, releasing abundant acids and lowering the pH. Leaves with mild (i.e. less acid) organic matter are quickly mineralized and humified, and they release abundant bases which are rapidly taken up by the growing plants. There may also be more directly active chemicals released by the vegetation which

facilitate territorial dominance by certain species. These were first noted in the walnut tree, which releases a compound (juglone) that somehow effectively prevents the growth of competitors. Similar compounds have been demonstrated in many land plants from the lichens to many forest species. These antagonistic reactions between species, and between individuals of the same species, may be very widespread, as we have undoubtedly not identified all of them. For example, the bracken fern has evolved mechanisms of toxin release that allow it to exert dominance most effectively in each particular habitat in which it grows. It is also, of course, widely toxic to large herbivores, producing internal bleeding and disturbance of vitamin metabolism. Altogether this represents a most formidable armoury of aggressive metabolic traits, possibly accumulated over many millions of years of evolution (Gliesman 1976, Taylor 1985). Complex allelo-pathic interactions have also been demonstrated in eight common species from British permanent grassland in which no obvious signs of allelopathic interactions were present (Newman & Rovira 1975). Of the four grasses in the set, *Anthoxanthum odoratum*, *Cynosurus cristatus*, *Holcus lanatus* and *Lolium perenne*, the first three were inhibited by leachates from other species. The forbs *Hypochoeris radicata*, *Plantago lanceolata*, *Rumex acetosa* and *Trifolium repens* and the grass *Lolium perenne* were inhibited by leachates from plants of the same species. Subsequent field observations have shown that the most auto-inhibited species are normally found as isolated individuals or only a few individuals in a group, not as pure stands. The three species that were allo-inhibited are all capable of dominating a permanent grassland. Allelopathic interactions have also been found to exist between herbs and woody plants (Horsley 1975). It has been shown, for example, that some plateau areas in the Allegheny Mountains failed to establish forest even 50 years after clearance and were dominated by a vegetation of bracken fern (*Pteridium aquilinum*), wild oat grass (*Donthonia compressa*), goldenrod (*Solidago rugosa*) and flat-topped aster (*Aster umbrellatus*). Experimentation eliminated browsing, microclimate and competition for light, minerals and water as explanations for the failure of forest regeneration. Subsequent experiments established that foliage extracts of fern, goldenrod and aster inhibited seed germination of black cherry (*Prunus senotina*) and that aster foliage inhibited both root and shoot growth of black cherry seedlings growing on their reserve of cotyledonous food. Similar effects have been observed on sugar maple (*Acer saccharum*). (An example of allelopathic interaction is shown in Figure 6.6.)
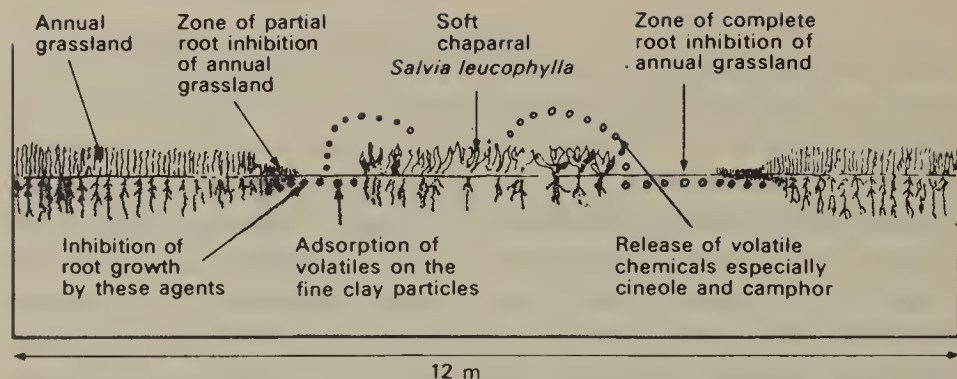
Figure 6.6 Allelopathic interaction between vascular plants, California. (Data from Muller.)

The converses of allelopathy are directly commensal or symbiotic associations, and these have only rarely been demonstrated in higher plants, although symbiosis is clearly frequent between higher and lower organisms. One example that has been shown is in the eastern white pine in New Jersey, where root grafting takes place in some conditions between adjacent trees. Radioactive tracers injected into one tree turn up in adjacent ones without entering the soil, indicating a possible sharing of resources (Billings 1964).

Plants also prepare the way for each other by building energy and nutrient resources into the soil as a plant *succession* develops. The first colonizers on soils derived from low-nutrient parent material or on very acid or very alkaline soils tend to be low producers. As these draw up minerals from the lower soil levels and involve them in the nutrient cycles, they build up the stock of nutrients in the soil so that colonization becomes possible for plants with higher productivity.

From all that has been said so far on plant–soil interrelationships, the reader will be aware that to establish causal relationships between plant distribution and substrate chemistry is not a simple matter. Clapham (1969) expresses this well when he says that 'Ecologists find themselves faced by the full and daunting complexity of the plant/soil system when they set out to understand what part mineral nutrition plays in determining the facts of species distribution.'

6.4 Soil classification

To render the task of establishing causal relations between plant distributions and mineral nutrition less 'daunting', it would obviously be of great assistance to have a coherent view of the ways in which soil characteristics change from place to place. However, this is not

possible because there are a number of opinions as to what are the most significant characteristics of soils for the purpose of classification. Broadly, these fall into two groups: (a) those which place emphasis on objective criteria based on intrinsic soil characteristics and aim at a zonal application on a large scale; (b) those which treat the soil more empirically and classify it according to its nature as a medium for plant growth. The first group can be exemplified by classifications such as the US Department of Agriculture's 'Seventh Approximation' and the FAO/Unesco system. These rely particularly on the **profile** the soil presents vertically. From the surface down to the unweathered rock, a particular soil will contain a number of more or less distinct horizontal divisions (**horizons**) whose depth, colour, chemical characteristics, etc., can be used to define the *soil type*. As developed in the USSR particularly, the major zonal soil type is presumed to be largely a result of climatic conditions within a major regional climatic type. Many of the terms derived from Russian practice are very familiar to western Earth scientists, for example podsol (Fig. 11.2), chernozem (Fig. 13.2) and rendzina. Terms derived from the Seventh Approximation and the FAO/Unesco classification may be less familiar and there is a considerable overlap between them so that a number of terms may describe the same soil type. Thus a grey podsolic soil (i.e. a thin, acid, leached soil with well marked horizons) is termed an *acrisol* in the FAO system and an *ultisol* in the Seventh Approximation. Table 6.1 lists some equivalent terms for important soil groups.

A number of workers have argued that as holocoenosis is inherent in the soil–plant–atmosphere system, such zonal classifications are not particularly helpful in making sense of plant distributions, as in some cases at least it is 'zonal vegetation which determines the finished product' (Eyre 1968). Whether the argument can be carried quite so far as to render zonal classification redundant is doubtful. As Burnham (1975) points out, in the tropics there is still no real substitute for the zonal view if a coherent account is to be rendered of the soils of a large region.

Workers who have tried to present a more empirical approach include Milne (1935), Wilde (1958) and Webb (1968). The views of Milne have had considerable influence in the study of tropical soils especially. Here the most significant factor to be established in relation to a particular soil is the position it occupies (*site*) in the suite of soil types (**catena**) that can be observed so frequently on slopes in the tropics (Fig. 6.7). Within such a catena, loss of nutrients by downslope leaching would be observed at the top of the slope and

Table 6.1 Equivalence of terminology and pedogenic associations of important soil groups* (Fitzpatrick 1980).

FAO name	USDA name	Other names	Climatic characters†	Vegetational associations
Transect A Arctic Russia to the Caspian Sea				
gelic gleysol	pergelic cryaquept	cryosol, cryic gleysol, tundra soils, tundra gleysol	PE: 100 mm or less T: below 5°C P: below 500 mm	tundra of grasses, sedges, lichens and mosses; in central Siberia, conifers, especially *Larix dahurica*
histosol	histosol	peat, bog soils, organic soils	PE: 100–300 mm T: 3–5°C P: 400–600 mm (in northern high latitudes)	associated in northern high latitudes with specialized bog mosses (*Sphagnum* spp. particularly), grasses and sedges; in lower latitudes with specialized trees, as in basin peats of Florida Everglades and coastal humid tropics, for example Guyana and western Borneo
podsol	spodosol	podsol in most systems	PE: 200–300 mm T: 4–8°C P: 500–700 mm	coniferous forest (boreal type) especially; can be induced by acid, mor-forming litter, e.g. under Kauri pine in New Zealand, beech in Great Britain and southern Sweden
luvisol	alfisol	argillosol, grey-brown podsolic	PE: 250–350 mm T: 6–8°C P: 750–850 mm (in northern high latitudes)	mixed forest of conifers and deciduous angiosperms; can be found with associated vegetation in tropical wet–dry, humid subtropical, mediterranean and humid continental climates and also as 'fossil' soils in formerly humid now arid areas
podsoluvisol		supragleysol, grey-brown posolic, sols lessivées glosiques	PE: 400–500 mm T: 7–8°C P: 750 mm	deciduous forest of humid temperate zones; in Europe, where this has been cleared they are in permanent pasture or heathlands
phaeozem	udoll	brunizem	PE: 500–650 mm T: 8–9°C P: 650–850 mm	in Europe, deciduous forest (*Quercus* spp.); in North America, tall grasses, e.g. big bluestem (*Andropon furcatus*)
chernozem	mollisols	chernozem is widely used in other classifications	PE: 750–900 mm T: 9–10°C P: 500–700 mm	tall grass with some deciduous forest in transitions from forest to grassland

A transect further west in central Europe would intercept another major world soil type

cambisol	inceptisol	brown earths, altosol, sols bruns	marine west coast or humid continental climates	deciduous forest on materials subjected to periglacial conditions before 10 000 BP; they also occur in many tropical areas
kastonozem	ustoll (mollisol)	chestnut soils, brown and dark brown (Canada), prairie soils (Australia)	PE: 1000–1200 mm T: 10–12°C P: 100–500 mm	predominantly mid-latitude steppe grassland
solonetz	many sub-divisions	many subdivisions in Australia, solonetzic (Canada)	PE: 1100–1300 mm T: 10–13°C P: 150–250 mm	formed by the progressive leaching of solonchaks which are deficient in calcium but contain large amounts of sodium ions; plant cover usually restricted (see text)
solonchaks	used in virtually all systems		PE: 1300–1400 mm T: 13–14°C P: 100–200 mm	varies from fairly dense to absent; plants usually have a high ash content of sodium, chloride and sulphate (see text)
xerosols	typic aridisol	desert soils, sierozem	PE: 1400 mm T: 9–10°C P: 100–150 mm	varies from continent to continent; in Eurasia, annuals and succulents dominate; in America, low xerophilous woody plants and succulents; in Africa and Australia, scrub woodland with many *Acacia* species

(contd)

Table 6.1 contd

FAO name	USDA name	Other names	Climatic characters†	Vegetational associations
Transect B Eastern Nigeria to central Zaire				
vertisols	vertisols	grumosols, pelosols	PE: 1400–1500 mm T: 15–17°C P: 100–300 mm	tropical semi-arid plant communities with tall grass and acacia thorn forest (teak forests in Java occur on these soils); ironstone (from plinthite/laterite‡) may occur as erosion has removed upper layers of 'fossil' ferralsol formed in more humid conditions
arenosol	psamments	sands, red and yellow sands, sols minéraux bruts	as above	tropical savanna and deciduous tropical forest developed over coarse sands; termite activity may play a major part in their formation, i.e. when a termite mound collapses, the fine sand may wash out leaving coarser materials
ferralsol	okisol	latosol, krasnozem, sols ferralitiques	PE: 1300–1400 mm T: 20–25°C P: 1000–1500 mm	rainforest and semi-deciduous forest; soils usually found below 1200–1500 m; most are at least of mid-Tertiary age; late Tertiary or Pleistocene deposits have a lower content of weatherable minerals; can occur outside usual climatic range and may carry thorn forest, savanna or deciduous woodland

*Important soil groups not included are: rendzinas (USDA, rendolls), which occur over limestones in widely differing climatic zones; regosols (USDA, orthents, psamments), which as their name suggests form on unconsolidated material (excluding recent alluvial deposits) and are the inception form of many soils; rankers (USDA, lithic haplumbrepts), thin coatings of soil on rock near the surface; andosols (andepts), which derive from recent volcanic material; and nitosols, which are strongly weathered tropical and subtropical soils with a steady increase of kaolinitic clay with depth but without the ferric properties of ferralsols.

† PE = mean annual potential evapotranspiration; T = mean annual temperature; P = mean annual precipitation.

‡ Laterite is a term applied to a soil horizon that is hard or will harden on exposure. It is highly variable in colour and texture but usually contains mainly oxides of aluminium and iron plus quartz, kaolinite and manganese oxides.

Oligotrophic, red,
non-swelling soils
with kaolin

Cuirasse or shield
of hardened ferralitic
material ('fossil ferralite'
or 'lateritic cuirasse')

Mesotrophic soils
with developed
profiles

Eutrophic, black,
swelling soils
(with montmorillonite)

Parent material

Nutrient downwash
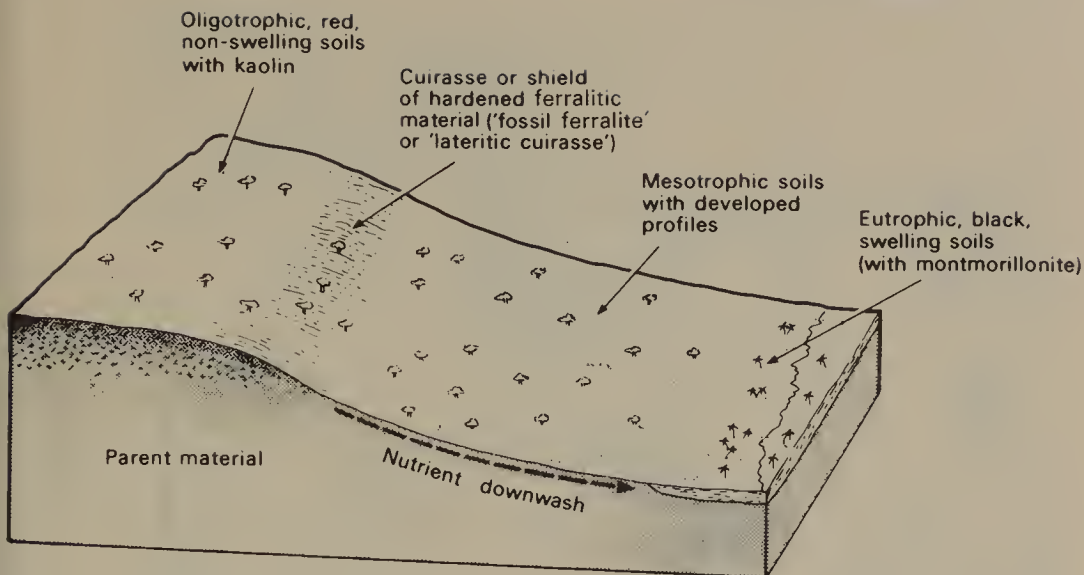
Figure 6.7 A tropical soil catena. (Terminology after Milne (1935) and Webb (1968).)

enrichment at the bottom, with corresponding vegetation changes.

The approach of Wilde, on the other hand, is based firmly on the nutrient status of the parent material in relation to forest soils. Thus rocks like sandstone and siliceous shales yield few nutrients when compared with parent material like granitic rocks, which may be low in only a few nutrients (phosphorus, calcium and magnesium), or basaltic types, which are nutrient-rich. However, in places like Britain or large areas of North America, where the surface is often mantled by glacial drift derived from a hotch-potch of rocks, the classification tells us little about nutrient status.

Webb has attempted a compromise between these two views and established categories similar to those long used by ecologists for aquatic habitats. Thus he identifies **eutrophic** types enriched by downslope movement of nutrients or on nutrient-rich substrates, **oligotrophic** types on nutrient-poor parent material or upper slope sites, and mesotrophic or eutrophic–mesotrophic types between the other two. By applying these categories in conjunction with vegetation analysis, Webb was able to achieve a unified classification of the soils and vegetation of the whole of the eastern Australian rainforests. This study was also able to demonstrate the clear link between the soil–plant system and the incidence of fire, an extremely important component of the atmospheric limiting system in that part of the world.

Australia also provides some of the clearest examples of plant

Frequent A

Ferralites · · · Podsols · · · Some gelic gleysols · · · Mostly gelic gleysols

+ Ironstone   × Solonetz   °° Solonchaks
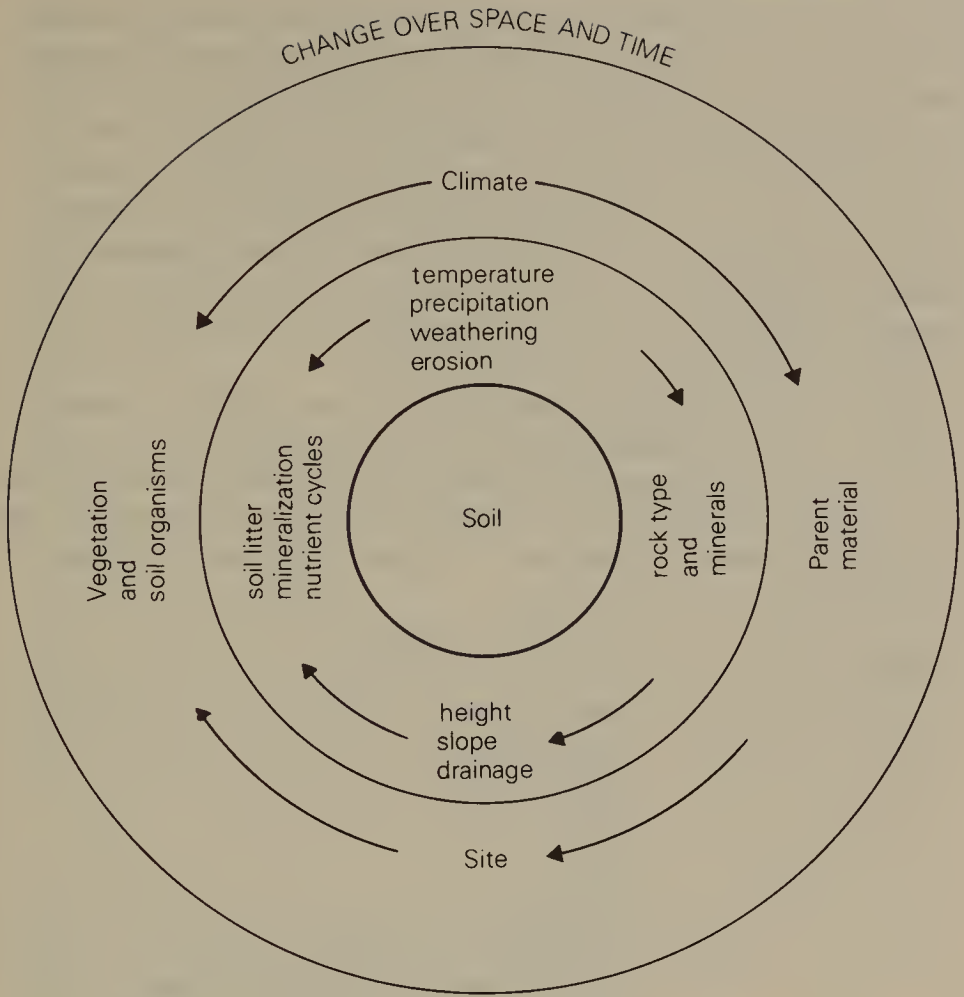
Figure 6.9 Interaction of the major environmental variables influencing soil characteristics.

species that over a long period of evolution have become closely associated with particular soil types. The genus *Eucalyptus*, for example, has around 365 species on that continent and each seems to have an optimum habitat and soil type. Brigalow (*Acacia harpophylla*) is also associated with particular soils, mainly vertisols.

However, in many parts of the world it is not possible to draw simplistic, causative inferences about the connections between vegetation and soil type distributions (Fig. 6.8). As indicated in Figure 6.9, changes over time in climate, vegetation, weathering processes and erosion rates, especially during and since the Pleis-

Figure 6.8 Distribution of some major world soil types: A, acrisols; C, chernozems; V, vertisols; Ca, cambisols; L, luvisols; P, frequent podsols. (After Fitzpatrick (1980).)

tocene, have meant that, in many parts of the middle and high latitudes, any long-term equilibrium that might have been possible between soil and vegetation has been thoroughly upset. Even quite low latitudes have been affected. For example, in south-east Australia at least five cycles of erosion, deposition and soil formation can be identified, with one soil type superposed or adjacent to another, forming an intricate and complex surface pattern (Butler 1959, Fitzpatrick 1980). In each of the cycles, because of the variable climate obtaining at the time, a different major soil type was generated (Table 6.2).

It will be clear from this section that to draw simplistic causative inferences about the connection between vegetation and soil distribution is not possible. It is only by careful analysis of the ways in which the atmospheric, plant and soil systems interact and are unified at particular places that correct connections between plant distributions and soil differences can be made.

Table 6.2 Generation of soil types in south-east Australia.

Erosion cycle	Soil type
K_1	phaeozems
	kastanozems
K_2	nitosols
	vertisols
K_3	acrisols
	nitosols
	solodic planosols (soils on level sites with poor drainage, strongly leached solonetz)
K_4	planosols
	solds
K_5	old weathered soil remnants

6.5 Plants and soil salinity

Probably the most extreme soil chemistry conditions experienced by plants are those where saline soils occur. Although there are no completely satsifactory criteria for defining the degree of salinity of a soil, it can be said broadly that where sodium is more than 50% of the total cations in solution, the soils are usually strongly alkaline (pH 9 or more), compact and airless, and sodium carbonate forms easily (*solonetz* soils). Where percentage of sodium cations is less, the soils are less alkaline (pH 8.5) and have a good crumb structure (*solon-chak* soils). Under arid conditions, salt, gypsum or lime crusts may occur on the former types.

According to their response to salinity, plants are conventionally classed into intolerant *glycophytes*, *glycohalophytes* able to withstand moderate salinity – cotton, date and barley are examples – and *halophytes* which find their optimum growth condition in saline soils. The common seashore plants such as glasswort (*Salicornia herbacea*) and seablite (*Sueda maritima*) are true halophytes.

Physiologically, salinity acts on plants in two main ways. In the first place, the large amounts of dissolved salts lower the water potential of the ground water, making it more difficult to obtain. In addition, the dissolved salts adversely affect nutrient absorption, or even have toxic effects where there are high concentrations of Cl^-, HCO_3^- and Na^+ ions. In particular, in plants without metabolic adaptation, the salts inhibit enzyme reactions, especially. In relation to the last effect, enzyme reactions would be inhibited in glycophytic species by a content of Cl^-, HCO_3^- and Na^+ at levels far below those found commonly in halophytes.

The lowered osmotic potential of ground water heavily impregnated with salt is overcome in most halophytes by the establishment of a sufficient concentration of solutes in the cell sap to ensure that an osmotic gradient from soil to root can be maintained. In tidal saltmarshes, the osmotic potential of sea water is about -2500 kPa ($= -25$ bar $= -25.8$ atm) but in deserts, where evaporation is high, the osmotic potential of concentrated groundwater solutions can be many times lower than this. For example, the sap of *Atriplex* spp. has been shown to have an osmotic potential of -20000 kPa (-200 bar $= -202$ atm) on the edges of the Great Salt Lake in Utah.

The lodgement of otherwise harmful amounts of salts in the cell sap creates another physiological problem for plants. The osmotic potential of the cytoplasm itself must be maintained at a sufficiently low level to prevent dehydration. This is solved in most halophytes through the generation of solutes such as alcohols and nitrogenous compounds that can be accumulated harmlessly in the cytoplasm.

The ions absorbed in excess in many halophytes are transferred to the shoot and leaves. In some, salt is accumulated over the growing season or over the lifetime of the leaves and shed with leaf fall, for example *Juncus gerardi* (Sutcliffe & Counter 1962). In others, the salt content is regulated by the accumulation of water, resulting in a succulent habit. Many desert halophytes such as cacti are of this type, as also is the common saltmarsh plant *Salicornia* (glasswort). Regulation of salt content also takes place through salt excretion by epidermal glands. *Spartina* spp., *Limoniun* spp. (sea lavender) and some mangrove plants have evolved this method of regulation. The

actual process of excretion is still obscure, but is undoubtedly one that requires metabolic energy.

Finally, amongst adaptations to saline soils there is some evidence that certain plants, for example *Atriplex confertifolia* (shad scale) and *Artemisia tridentata* (sage brush), may be able to curtail the ingress of salts directly, but again the mechanism of this process is not fully understood, and it is not known whether it is more widespread in other species.

6.6   Mineral cycles and erosion rates

The cycling of nutrients under the control of plants affects soil erosion rates but, in spite of the considerable development of geomorphological science during this century, very little was known about it until relatively recently. The most important quantitative experimental work on the interaction of biogeochemical cycling and erosion rates, which revealed their intimate connection, came with the publication of the results of the famous Hubbard Brook watershed experiments in New Hampshire. In 1964 Borman, Pierce and Likens began a long-term study based on the experimental manipulation of small tributary watersheds in the 3076 ha area of the Hubbard Brook catchment basin. The area, with a fairly uniform geology, soil, vegetation and climate, proved ideal, particularly as it was already long established as a USDA Forestry Service experimental forest and had climatic and streamflow measurements for some 10 years previously. Calculations indicated a weathering rate of around 800 kg ha^{-1} y^{-1} of the granite and glacial till that composed the parent rock. The output from the watersheds via downslope movement and stream transport indicates that under present climatic conditions the surface would be lowered by around 0.03 cm y^{-1} (possibly 50 cm in the total period since afforestation following the last glacial epoch – 14 000 years). The same studies have also shown how important is the nutrient rain from the atmosphere to plants. The average figure in total is around 51 kg ha^{-1} y^{-1}, composed of varying amounts of calcium, sodium, magnesium, potassium, chloride, silica, sulphate, nitrate and ammonia. The last three components represent about 75% of the total and together with potassium are clung to tenaciously by the ecosystem. They have also been able to demonstrate the effects of both atmospheric pollution and pollution control. For example, by 1979 the total lead content of the forest floor in the study area had reached 8.6 kg ha^{-1}, but from 1975 to 1982 the concentration of lead in bulk precipitation fell by around 70%, a fall that correlates with the advancement of emission control on automotive

vehicles. At one stage in the mid-1970s, the workers were seriously questioning the continued existence of forest ecosystems of this kind should lead continue to accumulate in the soil at the then observed rates. (The reader will find a comprehensive guide to the numerous papers that this study has generated in Likens (1985).)

Obviously figures derived from one sample area cannot be applied even to other similar humid temperate ecosystems. Sampling by many other workers in other environments is necessary to gain a quantitative picture of erosion rates around the world. Morgan (1985) has summarized these to give generalized ranges of erosion rates as shown in Table 6.3. There are a number of striking features

Table 6.3 Generalized ranges of erosion rates.

	Erosion rate ($kg\,m^{-2}\,y^{-1}$)		
	Natural vegetation	Cultivated land	Bare soil
China	below 0.20	15–20	28–36
USA	0.003–0.30	0.5–17.0	0.4–9.0
Ivory Coast	0.003–0.02	0.01–9.0	1–75
Nigeria	0.05–0.10	0.01–3.5	0.5–15.0
India	0.01–0.10	0.03–2.0	1.0–2.0
Belgium	0.01–0.05	0.3–3.0	0.7–8.2
UK	0.01–0.50	0.01–0.3	1.0–4.5

in this table. First, there is a lack of difference between mid- and low-latitude countries in erosion rates from below natural vegetation. Given the great disparity in climate and the significant differences in biogeochemical cycles, this may seem surprising. In fact, Belgium and the UK have slightly higher rates than the Ivory Coast. However, as well established ecosystems tend towards homeostasis, it might be expected that soil erosion rates would be minimized as part of this tendency, and this appears to be the case. Secondly, the accelerated rates from cultivated land are for the most part clearly in excess of rates below natural vegetation. However, the figures quoted for the United Kingdom indicate that this does not necessarily have to be the case. Finally, the figures given for bare soil indicate how vulnerable is the land surface without plant cover of any kind. Borman and Likens (1970), for example, soon discovered this in their catchment area experimental site. By clear-felling of the forest and spraying to keep the ground flora from regenerating, the weathering and erosion rates increased markedly, although they took great trouble not to break the ground. In other areas where tree-felling was carried out without the clearance of ground vegetation, they were also able to show the

important role that forest floor vegetation plays together with litter and dead plants in the maintenance of nutrient cycles and the checking of erosion before forest regeneration once more provides full protection. This work has led directly to recommendations for tree-felling practices that will maintain most of the stability of the natural ecosystem and minimize erosive damage (Likens 1985).

The figures given in Table 6.3 for cultivated land can give a false picture of soil erosion if they are considered apart from those for soil regeneration. Unfortunately, no generalized figures for this process are available for large areas of the world, although they do exist for some of the areas above. For example, in Britain the rate of topsoil renewal is around $0.1 \text{ kg m}^{-2} \text{ y}^{-1}$, which compares with mean annual rates of erosion in fields with slopes up to 11° and sandy or sandy loam soils – the most seriously affected – of around $2 \text{ kg m}^{-2} \text{ y}^{-1}$. It has only been realized relatively recently that these rates are increasing with changes of farming practices, and signs such as gullying are becoming frequent in, for example, the light soils of the East Midlands. In single storms, gully erosion can reach $15–19 \text{ kg m}^{-2}$. It is fairly safe to assume that, even in the most favourable conditions, soil erosion is liable to exceed soil renewal unless specific farming practices are employed to conserve topsoil.

Soil conservation farming techniques include rotation, contour ploughing (often in combination), terracing, manuring, mulching, preserving a grass cover, minimum tillage and ridge planting where crop residues are left in trenches on the land surface. Sample figures indicate how effective these relatively simple technologies can be. For example, contour planting of loess soils in Ohio can reduce soil loss under potato crops to as little as $0.2 \text{ kg ha}^{-1} \text{ y}^{-1}$ from $32 \text{ kg ha}^{-1} \text{ y}^{-1}$ where crops are planted up and down a slope of 12%. In Malaya, peppers grown on a terraced slope of 35% generate an erosion rate of $1.4 \text{ kg ha}^{-1} \text{ y}^{-1}$ as opposed to unterraced cultivation of the same crop on a similar slope where an erosion rate of $63 \text{ kg ha}^{-1} \text{ y}^{-1}$ is generated (Pimental *et al.* 1987).

Of course, gross substrate movement can be and is a normal feature of a number of environments and experiments have shown the effectiveness of a cover to bare soil in reducing the erosive force of raindrops in particular. It is these which produce most of the initial damage. For example, Hudson and Jackson (1959) demonstrated the erosive power of raindrops long ago in their famous mosquito net experiment. They showed over a six-year period on two adjacent plots, one with mosquito netting suspended above it so rain was converted to a fine spray, and one bare to the sky, that the rate of soil

loss from the former was 1.2 m^3 ha^{-1} and from the latter 141.3 m^3 ha^{-1}. The effectiveness of any ground cover in slowing erosion is not simply that of protection by a layer of vegetation: its height, the density of cover and the root density all play a part. For example, raindrops reach 90% of their terminal velocity on falling from vegetation only 7 m high. Moreover, as they slide from leaves they often increase in volume, rendering them more effective as erosive agents. Thus, in a high moist tropical forest, for instance, where very large drops may be shed from a considerable height from large-surface leaves, it is the lower storeys of plants that are the effective agents of soil protection. For example, Douglas (1967) has shown in Malaya that in one river basin with 94% rainforest cover the erosion rate is 0.21 kg m^{-2} y^{-1}, but in another river basin with only 64% forest cover the rate rises to 1.03 kg m^{-2} y^{-1}. He has also provided data to show the intimate connection of soil loss, climate and plant cover (Douglas 1976).

We may list the main natural kinds of surface disturbance as follows:

(a) Movement of unstable, immature soils as in screes and rock-slides, which encourages colonization by pioneer species adapted to forming large, tough mats bound by extensive, deep-seated roots (see Fig. 18.2).

(b) Frost-heaving of the surface, which may disturb roots and possibly prevent the growth of plants altogether. In moderate conditions, although mosses and lichens are intolerant, plants like Arctic willow (*Salix herbacea*) and mountain sorrel (*Oxyria digyna*) can become established and fix the surface against heaving.

(c) In arid lands, wind deflation and abrasion damage above-ground organs and expose roots, and wind deposition may bury plants. However, the latter condition may also encourage some species, as with marram grass and the drinn.

(d) Sheet and gully erosion is damaging to permanent vegetation in arid and semi-arid lands but is rare where an established ecosystem exists, even if the ground is bare. With agricultural clearance, the rates of erosion can be high. For example, in the USA, figures for total erosion under cotton cultivation show that a slope of only 8–10% can produce an erosion rate as high as 1 cm y^{-1}.

In less extreme circumstances than those outlined above, the

control on physical movement of the atmosphere and the subsoil is a function of the plants themselves. From the pioneer colonizers on any site to the mature vegetation, the tendency is for the stability of the surface to increase. Indeed, without this inbuilt tendency to stability, mature communities would not be possible at all. Thus, clearance for agriculture always brings with it the threat of soil erosion whatever the environment. Only if proper conservation techniques are built in to the agricultural system can it be minimized.

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7

Plants in communities and their distributions

In nature, each individual organism and the species population of which it is part must constantly make adjustments to the presence and needs of the other plants and animals that share the land with it. The pressures of living in a community, together with the adaptations to the non-living habitat factors dealt with above, are selective determinants in the evolution of the general range and size of a species. Within this general range, each individual plant must establish its own relationships with its neighbours as best it may within the limits of its genes.

7.1 The distribution of individuals in a population

The ways in which horizontal space is shared out between competing species to form communities with some stability has been given much attention over the years by plant ecologists, who have put forward a number of models by which this process may be understood. Latterly, adapting concepts already established in animal ecology, attention has been focused on *genetic strategies* as a unifying concept in ecology. A strategy has been defined as 'a grouping of similar or analogous genetic characteristics which occur widely among species or populations and cause them to exhibit similarities in ecology' (Grime 1979). In working out its relationships with the environment, not least its territorial distribution, each species has a repertoire of genetic strategies that are deployed through their phenotypic expression. This has been expressed by the phrase 'the ecological theatre and the evolutionary play' (Hutchinson 1965), but in this instance the drama is all crowd scenes and the actors have almost exactly similar lines.

Strategies in plants have some similarities to those in animals. For

example, amongst insects, juvenile and established phases may call for quite different strategies. However, plants have one complicating factor not present in animals, and that is the facility in many types for vegetative as well as sexual reproduction. In the evolution of genetic strategies, all the selective forces dealt with in the three previous chapters (the Wallacian forces) together with the (Darwinian) biotic forces of competition can be placed into two major categories: those which produce stress and those which produce disturbance (Grime 1979).

(a)   *Stress*. As illustrated in previous chapters, all plants on land are subjected to factors that limit their production and growth. In natural vegetation, it is probable that no plant ever has the optimum needs for light, water and nutrients fulfilled by its environment. Thus, all plants on land are subject to greater or lesser degrees of stress and the intensity and effect may vary markedly between mature and juvenile stages. The stress factor may present itself directly as shortages, for example of light, water or nutrients, or via competition for resources from other species or plants of the same species.

(b)   *Disturbance*. All the forces described in Chapter 5 together with herbivore feeding, disease and the now almost ubiquitous activities of human beings have the power to disturb any equilibrium that may be established between plants and their environment. The possession of genetic resources to tolerate disturbance must exist in species if they are not to succumb to these forces. Of course, the intensity of disturbance will vary widely from one habitat to another but all habitats present plants with some disturbing pressures.

Grime (1979) has suggested that plants may be grouped on the basis of stress and disturbance into three basic groups:

(i)   competitors, evolved in relation to low intensity of both disturbance and stress (*C*-selected);

(ii)   stress-tolerators, evolved in relation to low intensity of disturbance and high-stress conditions (*S*-selected); and

(iii) ruderals, evolved in relation to high intensity of disturbance but low intensity of stress (*R*-selected).

Grime suggests that the plants in (i) are broadly equivalent to the *r* strategists of MacArthur and Wilson's (1967) theory, the plants in (ii)

to that theory's K strategists and the plants in (iii) occupy the intermediate range of the r–K spectrum.

Grime also suggests that a fourth category – high intensity of both stress and disturbance – will have no corresponding viable strategy. This may not, however, be the case, as we have already seen that some plants of the high latitudes and altitudes are subject to both high stress and high levels of disturbance.

This three-fold classification postulates that C-selected, S-selected and R-selected plants will possess distinct families of genetic characteristics and respond to habitat conditions of stress and disturbance in distinctive ways. Competitive (C-selected) plants will show large and rapid changes in root : shoot ratio, leaf area and root surface area, whereas S-selected types will have slow changes in morphology of small magnitude, and R-selected plants will display a rapid diversion of resources to seed production rather than to vegetative growth.

In any part of the world, the factors of stress and disturbance are likely to show a gradation from higher to lower intensities through both space and time as plant assemblages develop. Individual species usually have optimal positions on such gradients. However, as previously demonstrated (Sec. 6.2), the optimal position for a species on any gradient may be far from the actual position that the species occupies. In any complex vegetation, therefore, the distribution of individual species in either space or time will represent a series of compromises between the deployment of their genetic strategies, expressed through the phenotype(s) of each species to capture its share of resources, and the external checks to occupation of the optimum niche for production. The most important of these external checks is competition from other species.

The study of competition in biology has had a rather chequered history since the days of Malthus and Darwin, to whom it represented a harsh mechanism to prove fitness to survive through the struggle for existence. At one stage, indeed, so difficult was this concept to apply that at least one author advocated its abandonment altogether (Harper 1961). The kind of head-on confrontation and its outcome that Darwin envisaged was shown experimentally by Gauze (1934) to produce the complete elimination of one of the combatants. This conclusion was expressed in a rule, which states that, if two species are competing for the same resources in the same space at the same time, one of them will be extinguished. It has gradually been realized that competition of this kind is, in fact, rather rare in biology, although, as humans have shifted plants and animals around the world, it has become more frequent. Only when the 'time drive' of

evolution (Fig. 1.4) is given a sharp turn, as, for example, with the appearance of a sudden pollution effect, the introduction of a vigorous new competitor, the exposure of a difficult soil type (such as an acid volcanic rock) or the advent of an extreme climate (such as an ice age), is the competition so fierce as to allow the phenomenon of dominance by a single survivor or only a handful of survivors to occur. Analogous conditions where dominance by only one or a few species might be expected would be represented by extreme environments (see Part 3). In most benign environments, the phenomenon of niche-space differentiation is the rule and, although some competitors may be more successful than others in that they top the 'league table' of species rank order (Fig. 7.1) as the most 'fit', they by no means eliminate other types in the classic Darwinian sense.

The concept that individual species distributions can be related to a model based on the interaction of genetic strategies with gradients of stress and disturbance has proved very fruitful, and Whittaker (1975), in particular, has modelled a number of studies on the concept.

How the area occupied by a species is related to its population as a whole is another dimension to the explanation for the presence of a particular species at a particular place. On a world scale, one of the oldest general theories is the 'age and area theory' of the British ecologist, J. C. Willis. This is an excellent example of a logically satisfying theory which, unfortunately, so rarely fits the facts that it cannot be supported in its original form. The theory is simple in
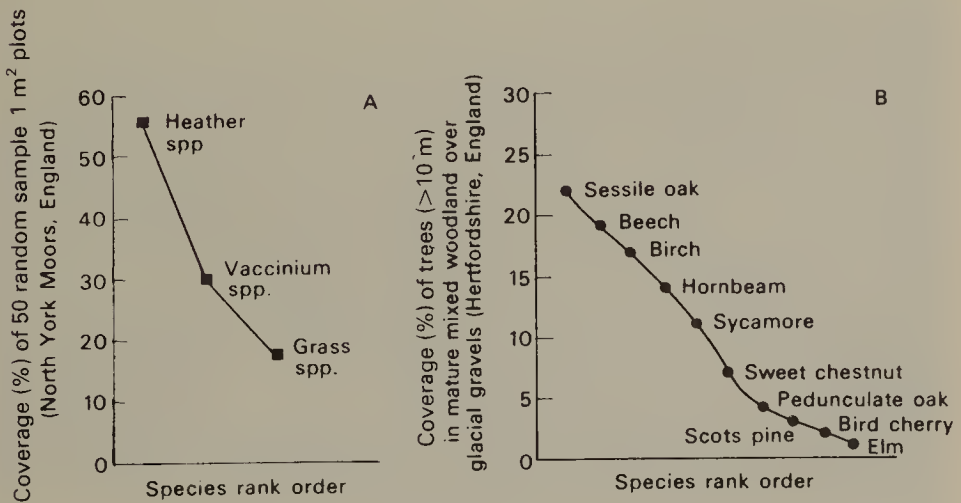
Figure 7.1 Two types of species importance curve. The situation in (A) is characteristic of plant communities in more extreme environments, whereas that in (B) is more characteristic of complex vegetation. The woodland from which (B) is derived is shown in Figure 11.1.

essence: statistically, the area occupied by a species is directly proportional to its age as a species, i.e. the longer it has had time to spread, the further it will go. Moore (1982) has argued that, although there is no evidence to support the original idea, nevertheless it could be useful as a concept in assessing the unequal oportunities that give rise to the many exceptions.

Theories based on the observed facts of species distributions and the correlation of these facts with other aspects, such as abundance, have received more attention in recent years. Two main relationships between abundance and distribution have been observed:

(a)   Population density of species tends to be greatest in the centre of the range of distribution and declines gradually towards the boundaries. This relationship holds over a variety of scales from the local region to the entire geographic range, although factors such as sharp, discontinuous changes in a single environmental variable and environmental patchiness can cause exceptions to the rule.

(b)   Amongst closely related, ecologically similar, species, i.e. those with similar strategies, spatial distribution is correlated with average abundance. Thus, if two species are deploying analogous strategies, the one with the greatest abundance on average will have the widest spatial distribution.

Brown (1984) has argued that a single general theory based on three assumptions can account for these facts. The three assumptions are: first, that both abundance and distribution of a species are limited by a combination of the physical and biotic variables that define the environmental niche; secondly, that it is likely that nearby sites tend to have more similar environmental conditions than more distant sites; and thirdly, that closely related, ecologically similar, species tend to have more similar environmental requirements than more distant species.

It is suggested from these facts and assumptions that the distribution of the population density over space should approximate to a normal probability density distribution, and, if the assumptions are violated, exceptions will occur.

Harper (1983) has argued that observations on the macroscale and theorizing on the basis of these are insufficiently reductionist. They ignore the actual facts of competition in the Darwinian sense in the life of plants. Until there are more examples of direct observation and experiments on the true ecology of plants, no valid theories can

Plate 1 Sheet erosion in the Upper Hunter Valley, New South Wales, Australia. Here the pasture has been overgrazed following clearance and ring-barking of the scattered trees. At the lower edge of the photograph the erosion is developing into a deep gulley. Notice the low angle of the slope on which the erosion has developed. (See Chapter 6.)
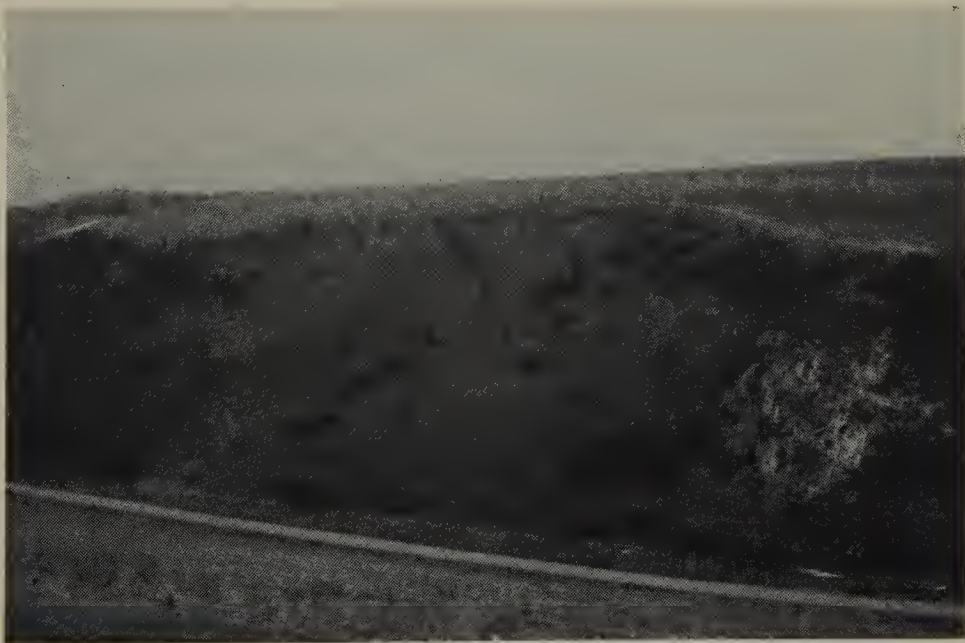
Plate 2 The grass-dominated fire climax slope shown in Figure 7.3. Note the outcrop of the Magnesian Limestone (dolomitic) on the right. Note also the invasive gorse (*Ulex europaeus*) which has become established since the fires caused by passing steam trains from the railway at the foot of the slope ceased when the line was closed in 1965.

Plate 3 Post-Pleistocene relict vegetation, Teesdale, County Durham, England. The dominant plant here is the juniper (*Juniperus communis*) and it has been maintained in this location because of the peculiarities of the local geology (an extensive outcrop of dolerite, called locally the Whin sill). It is probable that the juniper was originally the understorey of pine forests and has constantly regenerated from rootstock. (See Chapter 7.)

Plate 4 These so-called 'grass trees' in the Upper Hunter Valley, New South Wales, Australia, are indicative of the very distinctive botanical character of the Australasian plant kingdom. (See Chapter 1.)

Plate 5 Blanket peat developed over glacial clays, Teesdale, County Durham, England. The peat deposits began their development in this type of location with the onset of the Atlantic climatic type (see page 65) and are dominated by *Calluna*, *Erica* and *Vaccinum* species and various hardy grasses especially *Nardus stricta* and cotton grass (*Eriophorum spp*). (See Chapter 14.)

Plate 6 Alpine vegetation in Mount Kosciusko National Park, New South Wales, Australia. Note that in this continent the low tree vegetation is composed of hardy species of Eucalyptus ('snow gums') rather than the conifers familiar in the northern continents. (See page 299.)

Plate 7 Secondary forest developed over Permian limestone, County Durham, England. The land here was formerly used for cattle grazing and went out of production in 1928. From the pioneer shrub layer of hawthorn and elder the dominant ash (*Fraxinus excelsior*) is emerging. The photograph shows the vegetation at the western side of the slope shown in Figure 7.3.

Plate 8 Karri forest in Western Australia. The forest has grown in very nutrient-poor soils and both soils and vegetation have developed under a different climatic regime from that of the present. This is one of the most striking examples of 'vegetational inertia' on any continent. (See page 240.)

be properly or reliably formulated. As Harper puts it, what is needed is a 'plant's eye view of life and death'. Yet other authors have mooted the idea of coevolution of species and their distribution. McNaughton (1984) cites in evidence studies from the Serengeti, where grazing lawns below 10 cm height produced by the herds of animals have advantages in high productivity and quality and can maintain species distribution in the communities. In this respect, others have pointed to offensive–defensive interactions between herbivores and plants to explain population dynamics and distributions of species (Rhoades 1985).

The reader may conclude from the above brief survey, which by no means exhausts the theoretical answers to the questions 'Where?' and 'Why there?' in relation to species distributions, that the questions are not easy to answer. One of the main difficulties in formulating unequivocal answers to these questions is the indefinite nature of what exactly constitutes a plant community. At a fundamental level, as McIntosh (1978) points out, this question is commonly not only not answered but also not even asked.

7.2   Theories of plant communities

Through this century there have been various answers given to the question 'What is a plant community?' and it is still true that the study of plant communities (phytosociology) as a scientific study is bedevilled by different schools of thought as to how it should be done and what meaning may be attached to the answers. Schools may employ similar terminology with different meanings or a different terminology altogether, dependent on their view as to how plants behave collectively. These days they may employ complex information technology and mathematical techniques but to quite dissimilar ends. Broadly, during the century two schools were particularly persistent from 1900 to 1940: (a) the Braun-Blanquet (or Zuricho-Montpellier) school on the continent and (b) the Clementsian school in the USA. The former has at its core the concept of the plant **association** (inherited from 19th-century ideas and using the suffix '-etum' added to characteristic species) as the basic vegetational unit. The characteristic species were deemed to give a more positive indication of ecological conditions than the **dominants**, although the latter could also be characteristic species. These ideas, introduced in 1913, are still current on the continent, although they now employ automated means of identifying the characteristic species (Mueller-Dombois &

Ellenberg 1974). The Clementsian school identified succession as having the primary role in determining the character of communities. On this view the 'association' was the final stable or semi-stable climax community and placed emphasis on the dominants. The climax was assumed to represent the response of plants to the prevailing climatic conditions, and each climatic type would induce an appropriate climax community. Tansley in Great Britain, among others, modified this view – the 'monoclimax hypothesis' – by introducing the idea that several climax types could occur in a uniform climatic regime, especially in relation to soil or relief differences (the 'polyclimax hypothesis'). Both views tacitly assume that communities act as do human societies, that is in an integrated way (McIntosh 1978).

The two dominant schools represent, in fact, two methodologies in science. The first, with its patient sifting and comparison of species tables drawn up from samples, searched for the characteristic species to identify associations. This represents an inductive methodology. The second is essentially a deductive method derived from the supposed climatic climax type, and all vegetation would be related to this putative climax. Both methods are essentially classificatory systems.

In striking opposition to both these views, several workers in the USA, Italy, the USSR and France in the mid-decades of the century rejected both schools of thought. These views are usually exemplified in the literature by the American, G. H. Gleason (1926), who asserted the 'principle of the individualistic plant community'. On this view, in Gleason's own words, 'every species of plant is a law unto itself', the distribution of which, in space, depends on 'its individual peculiarities of migration and environmental requirements'; Gleason also stated that 'it grows in company with any other species of similar environmental requirements irrespective of their normal associational requirements'. This was a valiant attempt to 'demolish the whole system of arrangement and classification [of communities] and start anew'. Unfortunately, this valiant effort had no effect at the time and Gleason abandoned the field altogether.

It was not until the 1940s and 1950s that his views were recognized and developed further in the USA by a new generation of plant sociologists but, as yet, these views have had little impact in the prevailing continental school. Particularly prominent amongst these workers is R. H. Whittaker, whose gradient analysis methods and dominance–diversity studies, using the ordination methods developed by the so-called 'Wisconsin school' (Bray & Curtis 1957), are

firmly based on the individualistic concept of the plant association. Additionally, the concept of niche differentiation introduced from animal ecology has added a further emphasis to the individualist approach.

Whether 'continental' or 'American' in methodology, most phyto-sociologists would agree that, barring exceptional disruptions, most vegetation is essentially continuous in nature, but they still prefer to classify the most distinctive and recognizable groupings of species and habitats as associations. Salt (1984) expresses the two extremes of the approaches to phytosociology as follows:

(a) Communities are largely structured by random factors and therefore associations are incidental and accidental, and the making of generalized models about them is pointless (the extreme individualist point of view).

(b) Community structures are determined by a combination of (i) interference to species presence by the presence of other species both animal and plant, (ii) facilitation of species presence by the presence of others, (iii) change over space and time in resource quality, and (iv) alternative strategies of organisms at each trophic level.

The former view would be exemplified by the work of Horn (1975), who has shown that the success of trees in successional competition in temperate forests can depend on the statistical chances of success at the outset. The latter view would be exemplified by Rhoades (1985), who shows that the structure of a plant community can be significant-ly related to offensive–defensive interactions between herbivores and plants. In this he demonstrates that amongst plants there is a combination of strategies, from individual K strategists, which com-pete (interfere) strongly with other organisms at the same trophic level, to individual r strategists, which interact with other organisms minimally.

Some authors have gone even further than these views and rejected the notion that true answers to the question of the nature of plant communities can be deduced from temperate vegetation at all. They argue that only tropical vegetation represents the true norm of complex vegetation (Stott 1983). As Grime (1979) has pointed out in relation to basiphilous and calcicolous vegetation, the latter, in Britain at least, is much richer in species, as the former suffers from a reservoir effect. Along with others, Grime points to the differing evolutionary history of the two types as a factor. Calcicolous plants

have evolved mainly at lower latitudes in relation to high base-status soils generated in conditions of frequent high evapotranspiration rates. Moreover, from high to low latitudes, vegetational communities will tend to increase in complexity, first, as there is an increasing reservoir of species to draw on (as Figure 7.2 makes clear), and secondly, because of the longer period of comparatively uninterrupted evolution in low latitudes.

If it were true that the tropics are the proper field for the modelling of plant communities, this does not necessarily mean that the methods and insights worked out from temperate vegetation would be automatically invalid. It does mean, however, that the methods and models may need considerable modification in the light of tropical complexity, as some researchers have found (see Webb *et al.* 1967–70).
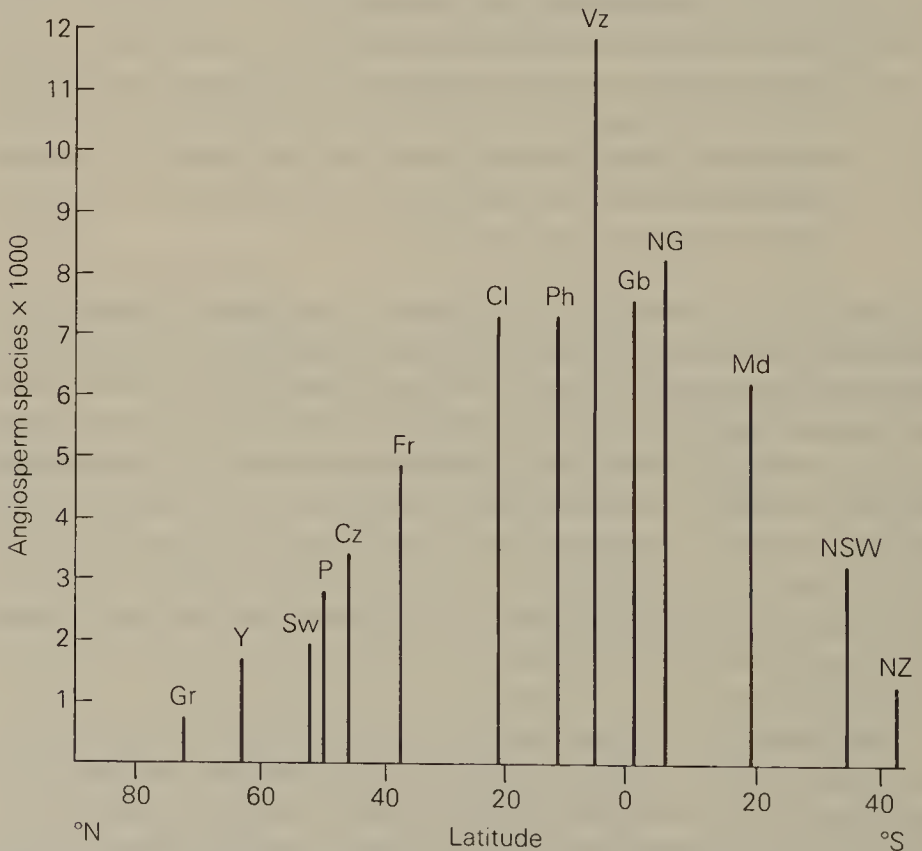
Figure 7.2   Absolute numbers of angiosperm species in the floras of various countries or regions: Gr, Greenland; Y, Yakut, ASSR; Sw, Sweden; P, Poland; Cz, Czechoslovakia; Fr, France; Cl, California, USA; Ph, Philippines; Vz, Venezuela; Gb, Gabon; NG, New Guinea; Md, Madagascar; NSW, New South Wales, Australia; Nz, New Zealand. Latitudes central to each country/region. (Data from Grime (1979) after Rejmánek (1976).)

Plant ecologists are in general agreement that the ways in which communities develop from initial colonization to climax vegetation may be described successfully by a number of models (Gibson & Brown 1985). These can be divided into two main types: (a) conceptual models and (b) mathematical models.

Conceptual models

These have been summarized by Connell & Slatyer (1977) and Gibson & Brown (1985) into four main types.

(i)   The first is the 'initial floristic composition' model, where succession is envisaged as proceeding from the presence of most of the species from the start. The course that is subsequently followed by the developing community will depend solely on the relative growth rates of these species, their reproduction rates, life-spans and so on. The model is exemplified by the work of Piroznikow (1983) on the deciduous broad-leaved forest of the Bialowieza National Park in north-east Poland. This, probably the least-disturbed remnant of the original climax hardwood coverage of northern Europe, is character-ized in the study area by dominant lime (*Tilia* spp.) and hornbeam (*Carpinus* spp.). Piroznikow found that the seed bank from which secondary succession could originate in smaller cleared areas was depleted of any species other than the main dominants. Some of the existing forest floor species, for example, were not represented at all and have persisted almost entirely by vegetative reproduction. Thus, succession in smaller cleared areas proceeds directly from the climax vegetation and the early successional stage as normally understood may be absent altogether.

(ii)   The second model is termed 'facilitational' by Connell & Slatyer (1977). In this case, early successional plants are those which produce considerable site modifications, particularly to soil charac-teristics. By litter trapping, alteration of drainage properties and nutrient enrichment, the soil is first rendered less suitable to the short-lived early colonizers, which effect these changes, but more suitable for longer-lived plants. These, in turn, may facilitate the entrance of other species. The facilitational model is particularly applicable to virgin sites where soil is rudimentary or very impover-ished (Fig. 7.3). Two examples may illustrate the process in both natural and artificial successions.

The first can be observed on coastal sand dunes in north-west Europe where plants such as sea couch grass (*Agropyron jun-ceiforme*), sea sandwort (*Honckenia peploides*) and saltwort (*Salsola*
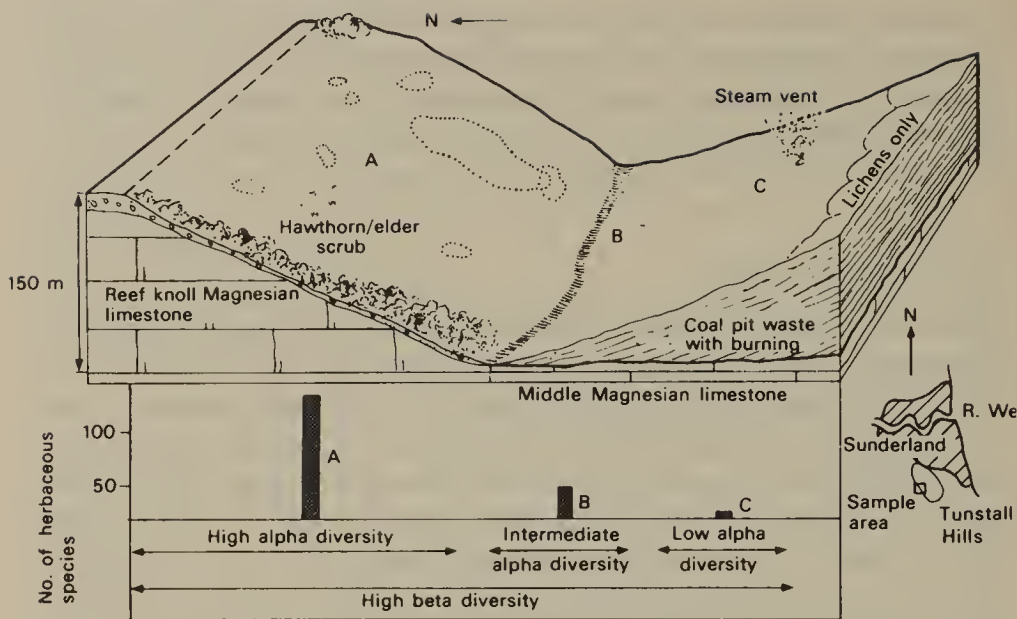
Figure 7.3 An illustration of alpha and beta diversity. (A) Limestone pasture dominated by blue moor grass (*Sesleria caerulea*) with many co-dominants and associated grasses, sedges and other herbs. Local co-dominance with other species indicated by dotted areas. (B) Mixture of species from area A with red fescue (*Festuca rubra*) and spreading meadow grass (*Poa subcaerulea*) important. (C) Skeletal soils dominated by coarse grasses especially cock's foot (*Dactylis glomerata*) and creeping bent (*Agrostis stolonifera*). Few insect-pollinated plants. Steam vents associated with moss (*Polytrichum*). Area A has been disturbed by frequent fires. (Alpha diversity = diversity within communities; beta diversity = change in species composition through space.)

kali) colonize initial blown sand. As windspeed is reduced by the rudimentary plant cover and more sand is trapped, saltwater inundation becomes less frequent and salt is **leached** downwards by rainfall. This allows plants such as marram grass (*Ammophila* spp.) to gain entry. These second-stage species are even more effective in the process of sand accumulation. However, the leaching process removes not only sodium chloride but also much more useful salts, and the developing soil becomes depleted in a number of vital nutrients, especially phosphates, which are out of reach of the grass roots. At this stage, the sward is not completely closed and sand patches are visible between the marram grass sward. This is often termed the yellow dune stage and other plants, sea couch grass, sea sandwort, sand sedge (*Carex archaria*), lyme grass (*Elymus arenarius*) and sea bindweed (*Calystegia soldanella*), are also found. As the dune matures, humus accumulation and further leaching produce a greyish soil and new immigrants, particularly lichens and mosses, grasses

such as red fescue (*Festuca rubra*) and sand sedge, become more abundant, together with ragworts (*Senecio* spp.), *Gallium* spp. and bird's foot trefoil (*Lotus corniculatus*). The landward side of dunes, the oldest section, may then acquire woody vegetation. In Anglesey, for example, Hodgkin (1984) found that the hawthorn (*Crataegus monogyna*) was able at this stage to tap the mineral phosphate leached downwards at an early stage in dune formation and the litter from this woody plant sufficiently enriched the soil that other woody plants could enter the late stages of the succession. In Britain, birch (*Populus* spp.) and oak (*Quercus robur*) may form the climax. The sequence in North America would be broadly similar to the above but with different genera and species. The shrub stage particularly would involve cottonwood (*Populus deltoides*), willows (*Salix* spp.) and pines, and the climax vegetation would include a greater variety of species than in northern Europe, for example, oaks, maples (*Acer* spp.) and hemlock (*Tsuga canadensis*). The mobile sands of tropical shores are frequently initially stabilized by plants such as members of the bindweed (*Convolvulaceae*) family, for example *Impomoea pescaprae*, which is the common pioneer species in south-east Asia. The tufted grass *Spinifex littoreus* and members of the legume family are also important. In south-east Asia the woody vegetation includes *Tournefortia* spp. and screw pines (*Pandanus* spp.). Climax vegetation in Malaysia frequently is pure stands of *Cassuarina equisetifolia* (ironwood). The last plant possesses nitrogen-fixing root nodules. (See also Chapter 18.)

The principle of facilitation has been successfully applied to land reclamation projects in many parts of the world. Bradshaw and his coworkers at Liverpool University, for example, by careful study of the genetics and physiological characteristics of pioneer colonizers, have devised seed mixtures of plants tailored to suit many intractable sites, for instance highly toxic mine wastes from lead extraction (Smith & Bradshaw 1979, Bradshaw & Chadwick 1980). In Cornwall, the barren, leached waste from China clay workings has been greened using a legume combined with judicious mulching to preserve water. Once established, the build-up of nitrogen allows other species to continue the succession.

Although the facilitation model usually results in the eventual establishment of a climax vegetation, there are situations where physical conditions are such that no clear dominant climax vegetation is possible. Watt (1947), for example, identifies cases where 'climax' communities may replace each other in rotation as the conditions for each facilitate the establishment of the other. This can be observed

on some raised peat bogs (Godwin & Conway 1939, Moore & Bellamy 1974, Foster & Fritz 1987).

(iii)   Connell and Slatyer's (1977) 'tolerance' model is regarded as having little evidential support and being difficult to apply to primary successions in any case. The model envisages that early 'succession-als' have no significance beyond being first in the field. Any subsequent developments merely reflect the changing fortunes of species under biotic competition without any temporal successional significance. It is suggested that it could apply to small-scale disturbances. In spite of theoretical strictures that the authors apply to the successional significance of this model, it does seem to reflect well the condition of, for example, some human-controlled artificial systems. The permanent pasture in North Wales extensively referred to in Section 7.3 could be regarded as an early successional stage fixed by the upland farming economy. Here biotic competition between the herbaceous species under the control of grazing ensures 'tolerance' between the species so that no one species can assume dominance.

(iv)   The final model is regarded as an 'inhibition' process whereby primary colonists exclude any competitor species. These can only become established in the system when early colonists die. Ultimately, the late successional stage is dominated by the latest-arriving types and the long lives associated with these effectively exclude species of the early stages as their niche space is occluded. The differing growth strategies associated with trees of early and late stages are most clearly expressed in the branching architecture of the two in both tropical and temperate vegetation, as shown in Figure 7.4 (Shukla & Ramakrishnan 1986, Marks 1975). It has been pointed out (Gibson & Brown 1985) that this model is well exemplified by vegetation of low productivity due to nutrient and/or water stress where the dominant species will fall into Grime's category of 'stress-tolerators'. Chaparral vegetation of the American south-west has been identified with this model (Biswell 1974).

Mathematical models

Because succession is often a more or less orderly progression through time (called a 'sere'), a number of workers have attempted to seek a basis for its description by the application of appropriate mathematical models. The most successful attempt has been the application of probability theory to the successional chances of any one species (or group of species). Horn (1975, 1976) pointed out that, if a matrix table of probabilities is prepared for the species or species groups that have an
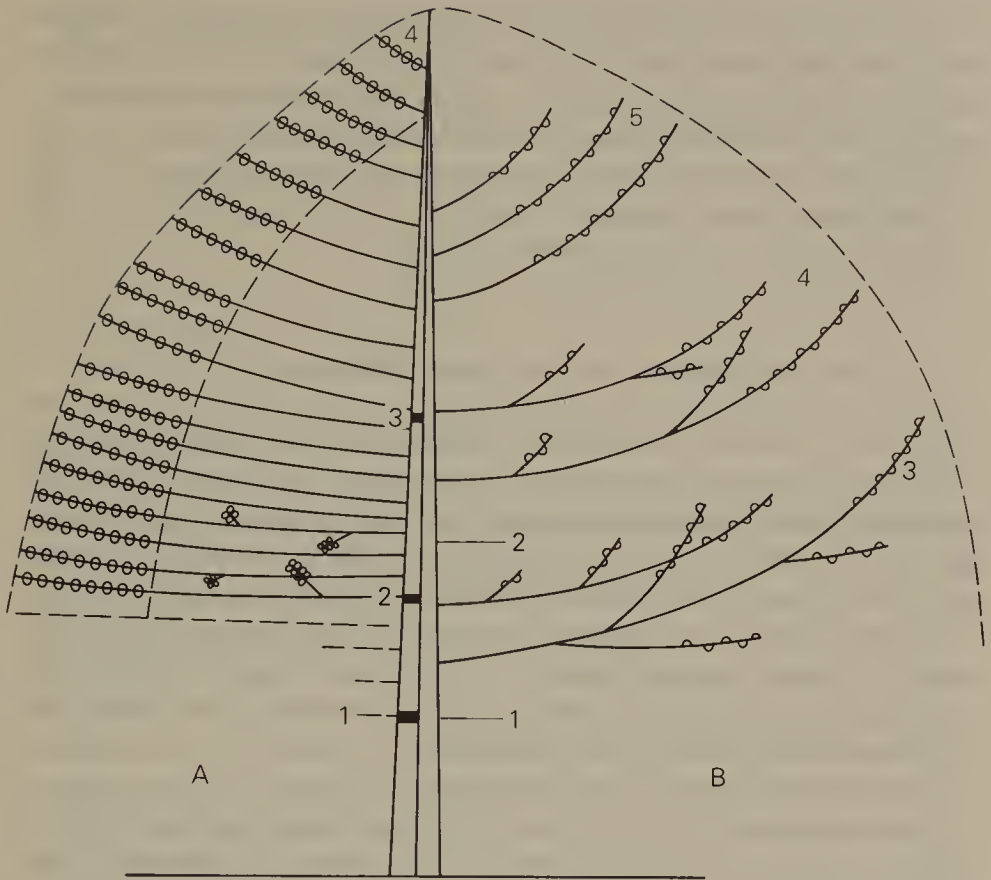
Figure 7.4 Architectural development of early and late successional trees from northern Indian tropical forests. (After Shukla and Ramakrishnan (1986). (A) Excurrent crown form of *Anthacephalus radambra* (early successional), four years growth. (B) Decurrent crown form of *Atocarpus chaplasha* (late successional), five years growth. Note in (A) self-pruning of lower branches. Note in (B) no branching in first two years growth but tiering of years 3–5 branching pattern.

available opportunity of becoming involved in a succession, then the progression (*Markov chain*) that results is very similar to what actually occurs in nature. The model can also be manipulated in response to a disturbance such as fire, which may change the species matrix or can be given an empirical value in relation to probabilities. However, although the matrix algebra is convenient, its application to real vegetation is (a) much more complex than the Markovian series can easily accommodate and (b) likely to be misleading and have a low predictive value (Austin & Belbin 1981, Gibson & Brown 1985). The model may be useful not for its intrinsic accuracy but for providing an indication of where it breaks down when applied to real vegetation. In fact, Gibson & Brown (1985) suggest that the real

utility of nearly all mathematical models is to 'be wrong in helpful ways'. As they point out, 'right' mathematical models are usually too complex to be convenient and are usually too narrowly restricted in application. Their healthy scepticism of the utility of mathematics is a salutary reminder that the living environment is usually many orders of magnitude more complex than can be encompassed by the reductionist purity of mathematical systems.

7.3   Plant demography and species distributions

Since the publication by Harper & White (1974) of their seminal paper on plants in relation to the demographic problems so long the subject of human demographic studies – birth, growth, reproduction and death – there has been a growing realization amongst ecologists that these aspects of the life of plants had been seriously neglected. That these studies are essential to give a full understanding of the ecology of plant species cannot be denied and Harper's (1977) text *Population biology of plants* has become a cornerstone of what to all intents and purposes is a new discipline.

One particular aspect that Harper has emphasized consistently is the much-neglected role of 'Darwinian' competition and its effects on plant populations and their degree of success in colonizing and holding territory. He has pointed out that much of plant sociology has emphasized the 'Wallacian' view of the plant and environment in seeking explanations of the ecology of plants. The 'Darwinian', reductionist tradition of concentrating on biotic competition has played little part until recently in modelling plant response in natural vegetation, in spite of some workers favouring it sporadically.

The essential feature in all such Darwinian work is the close observation of plant–plant and plant–animal interactions in permanent quadrats with an added dimension through Harper and his coworkers of precise experimental work. Harper's own work is the model for such investigation, concentrating as it has for decades now on one small (1 ha) field of permanent pasture at Henfaes, near Bangor in North Wales, chosen specifically for its unremarkable qualities. Studies have concentrated on the common species of the pasture especially *Trifolium repens*, *Lolium perenne* and various species of *Ranunculus*. The wealth of information and the subtlety of the scale of interactions between species that have been demonstrated are both surprising and daunting: surprising in that the sheer number of strategies displayed by these species in such a small

compass it totally unexpected, and daunting in that, if the scale of 1 ha can yield such complexity, what of the task of the larger scale?

Some brief examples from the work will illustrate the point. It has been discovered, for example, that in the field the distribution of *L. perenne* and *T. repens* are positively correlated, and negatively correlated with other species. On a Wallacian view the hypothesis might be that both species are responding to minute variations in soil quality in the same way, and the same hypothesis might be made from the individualist viewpoint. This does not, however, seem to be the case. The two species are positively correlated biotically, probably through some mechanism of facilitation. The species themselves primarily determined each other's distributions. One of the species, *T. repens*, displays clonal growth and its interaction with another species with clonal growth, *Ranunculus repens*, has been of particular interest. Because clones are produced from the product of a single zygote spreading by vegetative reproduction through the sward, the population of the species is likely to display clear expression of any polymorphic genetic variations. *T. repens*, for example, has yielded around 50 clones for the whole field, which were shown to be different for an average of 2.4 purely vegetative characters and 5.4 vegetative and floristic characters. (The most extreme difference amongst the 50 was one pair that differed by as much as 13 statistically significant independent characters.) Further polymorphic differences have been demonstrated in physiological and biochemical characters. Within each 1 m^2 quadrat, approximately 3–4 clones were present on average. Experiments in growing *T. repens* in association with rye grass (*L. perenne*) showed very positive effects. For example, a single clone of white clover grown with a variety of rye grass clones produced distinctive phenotypic modifications dependent on the rye grass strain.

Many plants possess this cloning habit and are able to dominate large areas. An extreme example is bracken fern (*Pteridium aquilinum*), which has been shown in northern Finland to have specimens 1440 years old, and in one case dominating an area as large as 474 × 292 m^2. Also, in the grassland forest ecotone in south-west Canada, the 'island' groves of aspen (*Populus tremuloides*) are almost all clones produced by vegetative reproduction.

Biochemical polymorphic variations have also been demonstrated as important in affecting distribution of the species. *T. repens*, for example, is polymorphic for the production of cyanogenic glucosidates in the leaves and this has been shown to be significant in relation to feeding by slugs. Cyanogenic forms occur more frequently

in areas of the field with high slug density and less frequently than expected in areas of low slug density, indicating positive selection of the 'defensive' form. Slug density itself relates to the presence of nettles (*Urticaria dioica*), which provide refuge for the animals from desiccation, thus adding a further dimension to the complexity of biotic interaction. In fact, about 1000 flowering plant species have the facility to produce cyanide in leaves and fruit, including the important food crop, cassava. (For an account of the interaction of cyanide with herbivores in bird's foot trefoil (*Lotus corniculatus L.*), see Jones & Compton (1985), and for a general account of plant–animal interactions, see *Oikos* (1985).)

The many other detailed studies of this 'superficially very dull' field, as Harper calls it, have revealed the subtlety of interactions underlying the macroscale models outlined in the two previous sections. Although studies such as those at Bangor do not invalidate the conclusions to be drawn from large-scale models, they illustrate that such 'Wallacian' approaches are only the first step in providing a framework of understanding of how communities of plants and animals interact. The reductionist 'Darwinian' approach is equally essential, revealing as it does the restless dynamism of plant–plant and plant–animal interactions from day to day and season to season within the relatively long-term timeframe of the community as a whole. The simple field at Henfaes, near Bangor, has remained apparently 'static' for at least 150 years, trapped in its 'Wallacian' frame of upland farming practices, but this stasis is now revealed to be completely illusory as the plant and animal populations pass through their life-cycles, restlessly competing with each other for their share of resources. Harper and his coworkers have done a great service to ecology in bringing the Darwinian plant's eye perspective back to centre stage in the 'ecological theatre'.

A further dimension to the question 'What is a plant community?' is the problem of how many species can a plant community contain. Are there any general limits and, if so, what factors affect those limits? (See also Sec. 3.1.)

Grime (1979) has put forward one answer with a general model based on many studies of herbaceous vegetation and comparing these with both tropical and temperate woody vegetation. This is the so-called 'hump-backed' model (Fig. 7.5), also called the 'window' or 'corridor' model. In this Grime identifies five major processes controlling species diversity in vegetation (dominance, stress, disturbance, niche differentiation, and ingress of suitable species or ecotypes) and suggests that the maximum species density bears a
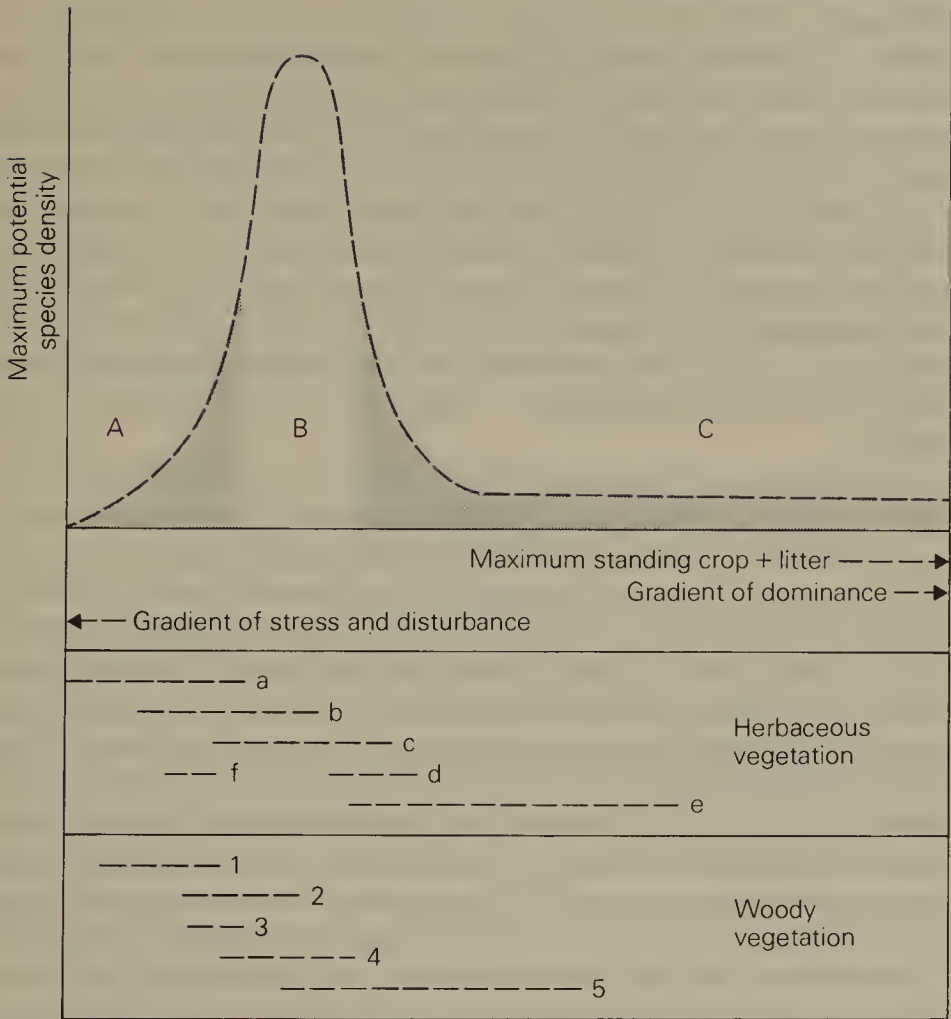
Figure 7.5 Relationship of species density and standing crop plus litter: the 'hump-back', 'window' or 'corridor' model. (After Grime (1979).) (A) Suppression of species diversity by extreme conditions of stress and disturbance. (B) 'Corridor' or 'window' of intermediate range in biomass with potential for high density of species through niche differentiation and ingress of suitable species of genotypes. (C) Species density suppressed by dominance. Note that this model gives only general relationships to be expected in any particular vegetation type. It is not possible to equate biomass figures from one type to another. Herbaceous: (a) paths; (b) grazed rock outcrops; (c) pasture on oligomorphic sites; (d) fertilized pasture; (e) pasture on eutrophic sites; (f) chalk grassland (southern England). Woody: (1) arctic–alpine scrubland; (2) temperate scrubland (e.g. macchi, chaparral); (3) temperate hedgerow; (4) species-rich tropical wet forests; (5) mature temperate, subtropical and tropical forest on mesotrophic and eutrophic sites.

relationship to the standing crop plus litter as shown in Figure 7.6. As can be seen, the model is comprehensive in that major vegetation types can be related to it. The model is further developed by

Whittaker (1977), who, impressed by the extremely high species density in pastures subject to centuries of grazing in Israel, adds the dimension of evolutionary time to the model. Given a very long period of stress, vegetation responds, first, by the emigration of new species (already included in the model), and, secondly, by evolution of the species present to adjust to stress. Thus fire, or grazing or whatever, become essential to maintaining species diversity when selection pressure has induced evolutionary change. Huston (1979) has also argued that frequency of disturbance is important to allow new species to become established, and therefore moderate levels of both stress and disturbance are necessary to maintaining species diversity.

Experimental evidence has an important bearing on the validity of these models, and there are a number of sufficiently long-term studies to provide some verification. The longest of these are part of the work carried out at the Rothamsted Experimental Station in Hertfordshire, England. Here the Park Grass experiment demonstrates that a grassland that has been mown and fertilized for decades, and where no reseeding has been allowed, has gradually lost species from its original composition of an average of 40 per square metre. This exemplifies what has been called the 'paradox of production' and indicates that optimal conditions for production are different from optimum conditions for species diversity. In Africa, another long-term experiment (begun in 1933 in the tall miombo woodlands near Ndola in Zambia) shows the effect on species composition of degrees of disturbance. During the half-century the experiment has been carried, out, homogeneous plots in *Brachystegia floribunda–Jelbernandia paniculata* woodland were treated in one of three ways: (i) late burning at the end of the dry season, involving a hot fire in dry, hot weather; (ii) early burning at the start of the dry season, involving a light burning; and (iii) complete fire protection. Plots treated as (i) had lost virtually all trees by 1944 but plots treated as (ii) maintained a woodland cover and normal species richness. Plots without fire quickly developed into a dry evergreen forest and lost species. A similar experiment in the Olokenji Forest Reserve in southern Nigeria showed similar results over a comparable period.

The above experiments tend to confirm, first, that a lessening of stress in relation to production tends to lower species density, and, secondly, that moderate disturbance tends to maintain species richness. Observations in natural vegetation tend to verify these results in both tropical and temperate lands. Huston (1980), for example, found that in Costa Rican rainforest there were consistent correla-

tions between species richness, precipitation, tree height and soil fertility, with the interpretation being that the vegetation with the highest species density occurs over poor growth conditions. Thus, in the world's 'richest' woody vegetation, the tropical rainforest, it would seem that this model provides a major key to understanding how so many species can be contained within them. The soils underlying them are notoriously poor in nutrient reserves and, as we have seen (Sec. 3.4), the turnover rate from natural tree fall is quite high. Thus, given the long period of evolutionary time for response to these factors of stress and disturbance to develop, plant life has generated the maximum species differentiation encountered on Earth.

7.4 Community analysis and classification

Because of the lack of general agreement about the theoretical basis of community behaviour, a number of different systems of analysis, classification and mapping have developed. Unlike topographic maps, however, where there is some general agreement about the data to be marked, vegetation maps are highly interpretive documents, often peculiar to the country of origin, the school of vegetational analysis, or even the individual worker developing his own ideas. The analytic and classificatory methods employed in vegetation study fall into three main types: physiognomic, floristic and ecological. Physiognomic systems, i.e. those based on the appearance of vegetation, have a long history but have been criticized by some botanists as being too imprecise to be really useful. Moreover, there is often confusion about terminology from one system to another, particularly where workers have attempted simultaneously to classfiy both the vegetation and the controlling environmental factors. For example, the term 'tropical montane forest', which implies connections with climate and site, has been widely used in the literature, but it has been noted that the limits assigned to it on various criteria span a range of no less than 2600 m (Robbins 1968).

In spite of these difficulties, most ecologists and geographers are led to the inescapable conclusion that the appearance of vegetation reflects fairly faithfully the sum total of all the ecological factors of habitat, and physiognomic methods are therefore by no means redundant. Also, there are still many parts of the world – and these are legion in the tropics – where precise knowledge of the interactions that control the nature of communities is so lacking that physiog-

nomic methods provide the primary means of access to the meaning of vegetational patterns (especially as they are particularly suited to aerial photographs). Moreover, since the launching of orbiting satellites, the maps that can be constructed from the data they generate allow rapid changes of vegetation to be accommodated. However, these, as well as maps from aerial reconnaissance data, need ground-level sampling to become reasonably reliable (Tucker *et al.* 1985, Goward *et al.* 1985).

The most sophisticated physiognomic system of vegetation analysis is associated with Küchler (1966) in the USA. It has been tested on different vegetation types around the world and sets out to overcome some of the disadvantages mentioned above. It is too complex to list here in its entirety, but it uses a standard terminology that is fairly unequivocal, does not require taxonomic knowledge and can be used in conjunction with maps of any scale, country or region. The system relies on letter and number symbols and letter combinations (formulae) to designate the various types of vegetation. This system is now widely taught and used in the USA, where its speed and efficiency, even when used by workers with little botanic knowledge, have proved its utility time and again.

Floristic methods involving much more specialized knowledge have been widely employed in continental Europe especially and are particularly associated with the Swiss phytosociologist J. Braun-Blanquet. The methods are often described as the Zuricho-Montpellier system, from the botanical schools with which they are associated. They require very precise botanical information before the classification can begin, and the ultimate aim is to produce a hierarchical ordering of all the community types of a region, which is presented as a species table. Although the methods have been criticized (Küchler 1967), the system has been successfully applied in both temperate and tropical lands. In the latter, however, attempts to apply the methods to lowland rainforests have met with little success (Longman & Jenik 1974). Indeed, many authors deny that the concept of the plant **association**, which is the basis of the community typing at which floristic methods aim, is applicable in any case to lowland rainforests.

Because floristic methods are so widely employed in the European literature and have a widespread influence on phytosociology, they will be dealt with below in more detail than is usual in treatments of this kind. It is important to remember that, although European and North American methods of processing phytosociological data are very different, they should ideally be regarded as complementary

rather than as alternatives. (Unfortunately, because of the different historical traditions, they are rarely seen this way.)

The Zuricho-Montpellier system

The aim of this system is to produce a floristic basis for the identification of communities (*phytocoena*). The phytocoenon is an 'abstract' community type that has been identified within the samples of the 'real' vegetation. A *phytocoenose* is an assemblage of the actual vegetation at a particular place. The identification of selected diagnostic species for characterizing these and the arrangement of the community units at greater and lesser scales are ordered into a hierarchical classification of units (*syntaxa*). The procedures are as follows.

(a)   Identification of the minimal area is first carried out. By reconnaissance in untested vegetation or by reference to precedent, the minimal area is identified as the smallest ground area needed for the community to develop its floristic expression. The area will vary widely from one vegetation type to another. In northern Europe, for example, in an oak forest it is around $200\,m^2$, in heather-covered heathland $16\,m^2$ and for acid grassland $9\,m^2$.

(b)   Choice and positioning of sampling units is the next operation. The sample unit (*relevé* or *Aufnahmen*) is positioned in uniform stands to cover an area larger than the minimal area.

(c)   Sampling is then carried out. All plant types are listed, together with an estimate of their cover using a code number. (Earlier work also used a code for sociability, but this is rarely done today.) Numbers for coverage are derived from a five-point scale: × = less than 1%; 1=1–5%; 2=6–25%; 3=26–50%; 4=51–75%; 5=76–100%.

(d)   A matrix or row table is prepared. This is organized in columns for samples and horizontal rows for species, with coverage code given at the intersections.

(e)   Manipulation of the raw data is performed. The rows and columns are reordered subjectively and manually, or by automated means, to reveal correlations of presence or mutual exclusivity between species, which can be used to order the samples into distinct groups to produce a final *differential table* (an example of which is shown in Figure 7.6).

(f)   The relevés may then be grouped into classes of unspecified rank called phytocoena. The percentage occurrence of each species is described as its *constancy* or *presence* in the samples of phytocoenon.

(g)   Each phytocoenon may then be condensed to a *synoptic list*, indicating the constancy of each species.

(h)   A number of lists can then be incorporated into a *synoptic table* by which a large number of phytocoena may be compared, enabling an estimate of the *fidelity* of each species to each phyto-coenon to be judged. Fidelity is estimated on a five-point scale: (1) *accidentals*, normally occurring outside the community; (2) *companions*, with no strong preferences for a particular community; (3) *preferentials*, normally better developed in one community but present in others; (4) *selective species*, much better developed in one community; and (5) *exclusives*, restricted to only one community. Species of ranks (3) to (5) are known as *characteristic species*.

(i)   Phytocoena can then be arranged in a hierarchical, formalized classification of vegetation called syntaxa, distinguished by suffixes. In descending order these are: sub-association (*-etosum*); association (*-etum*); alliance (*-ion*, with characteristic physiognomy and structure); order (*-etalia*); and class (*-etea*).

This rather long-winded procedure is only the beginning of the ecological study. The assumption underlying the order of the vegetation is that there are causative ecological factors determining the hierarchy and its geographical expression. It must be admitted, however, that many of the published studies often seem to present the classification as an end in itself rather than the beginning of scientific ecology.

Other classificatory systems

Those which have emerged at various times in this century include: the Uppsala methodology, developed by Sernander and du Rietz, based on stratification of vegetation and the dominants in each stratum; the British approach, developed by Tansley, where dominance defines the basic units, the associations; and eastern European methods, associated with such workers as Lippmaa and Sukachev, which identify the community (phytocoenose) as any plot of vegetation with uniform composition and uniform layer societies or *synusiae*. Strictly, a synusia is a group of plants occupying a specific habitat within a phytocoenose – broadly equivalent to the meaning of ecosystem – having a similar role, but not related taxonomically. The last system also recognizes the responses of the communities through areal variation of the synusiae as far as these can be related to both environmental gradients and genetic sequences. A useful summary of these can be found in Moore (1982).

Figure 7.6 Section of a differential table derived from phytosociological survey of the *Nothofagus* forests of southern Patagonia. Numbers 1–41 at the top indicate the sequence of relevés studied. The class is characterized not only by *Nothofagus pumilio* and *Nothofagus antarcticae* but also by the 15 other species listed. The numbers indicate cover: × = less than 1%; 1 = 1–5%; 2 = 6–25%; 3 = 26–50%; 4 = 51–75%; 5 = 76–100%. (After Wheeler (1982).)

Stimulated by the development of numerical taxonomy and the availability of digital computers, workers over the last two decades have applied a number of numerical techniques to recognition of phytocoena. Usually, the total floristic content of each sample is quantitatively assessed from the degree of similarity between vegetation samples, and two methods have been particularly important: divisive techniques and agglomerative techniques. The first is represented by *association analysis* (Fig. 7.7), which subdivides a set of samples into smaller classes of increasing homogeneity. The method was first not successful in its application to complex tropical vegetation (Webb *et al.* 1967–70), but an alteration of sample size later produced more satisfactory results in identifying units within the communities of tropical rainforest in Australia. The second group of techniques are based on *information analysis*, which involves manipulation of the data using similarity to agglomerate the samples into
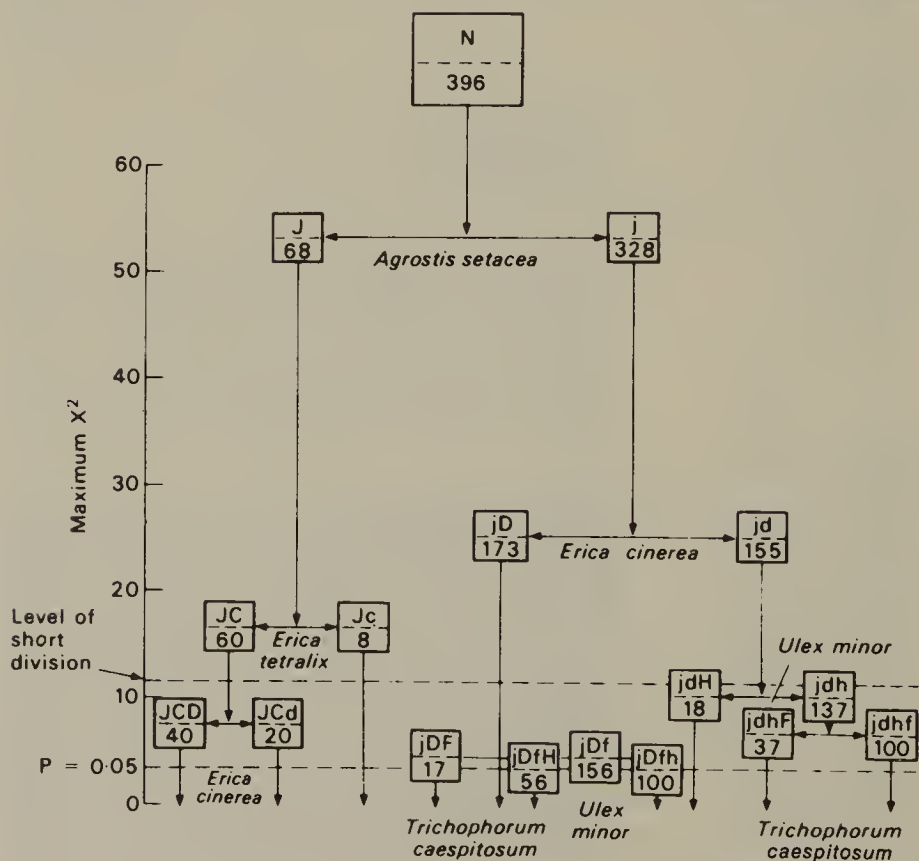
Figure 7.7 Normal association analysis to produce a hierarchy of 10 species in the New Forest. (After Williams and Lambert (1960).) Data are drawn from 360 quadrat sites. Species presence is indicated by capital letters, their absence by lower-case letters.

progressively larger units. One great advantage of both these techniques is that they can eliminate subjective bias in the choice of samples and can rely on random sampling. They can also be used in conjunction with some of the techniques of the Zuricho-Montpellier system.

Ecological–physiognomic system

To avoid some of the problems associated with both purely botanical and purely physiognomic systems, an ecological–physiognomic system has been devised, which is intended to provide an internationally acceptable system for vegetation classification. This has been adopted by Unesco (1973) but has not yet been universally accepted by all ecologists (Whitmore 1975). As with most systems relying on the appearance of vegetation, the basic unit of classification is the **formation**, i.e. a vegetation type distinguished by the unity of its structure, physiognomy and floristic composition. These may be grouped at a larger scale into **formation-type**s. Thus within the tropical Far East at least 13 distinct forest formations can be distinguished within the major formation-type of the tropical rainforests (Whitmore 1975). The assumption is made in this classification (and others that resemble it) that the formation structure and physiognomy are ecologically significant and represent a response to habitat factors. As to precisely what habitat factors may be significant and how they interrelate in many forest types, especially tropical ones, there is as yet limited evidence. In complex vegetation, it is probable that field observation will need to be supplemented by accurate model building and computer simulation of performance to reach adequate conclusions about the nature of habitat conditions and vegetational response.

Some US authors have preferred the term *ecosystem-type* to the term formation, implying a unity of all organisms within the ecosystem-types recognized. In European literature the terms *biocoenosis* (plants + animals + micro-organisms) and *biogeocoenosis* (biota + non-living habitat) are used in a broadly similar way. The broadly equivalent terms *biome* and *life zone* are also in frequent use in North America. However, whatever the terms used and concepts implied, the maps drawn by authors who use these terms usually resemble closely the familiar formations and formation-types of physiognomic analyses. This is not particularly surprising, of course. As plant life dominates the working of an ecosystem because it is the main channel for the disposal of energy and materials within it, it

might be expected to be used as the critical means of distinguishing between one ecosystem and another.

Methods of community analysis that have found favour in Britain and North America are concerned with ordering vegetational data in such a way that the presumed underlying ecological relationships can be more easily discerned. Collectively, these methods are described as *ordination techniques* (see Fig. 7.8), the word 'ordination' being defined as the 'arrangement of units in a uni- or multi-dimensional space' (Gittins 1968). It is also defined as an arrangement of units whereby their positions are determined by their properties (Wheeler 1982). Ordination embraces a variety of techniques, not all of them statistical. Thus, the familiar geographical transect is an 'ordination'.

As we have seen, the ecological factors that influence vegetation are multivarious and, therefore, the initial, subjective judgement to be made is the choice of important determinants at work in the particular types of vegetation to be subjected to ordination. Implicit in all the methods is the recognition that, although vegetational variation is continuous, ecological factors will nevertheless influence significant numbers of species to behave in related ways. The ordering may be based on any appropriate property of the total set of information, floristic composition, habitat factors, the population of a particular species, or whatever is deemed to be of significance ecologically. The arrangements of information that are made are essentially geometrical, using one of a number of axes to give a uni-dimensional ordination (the transect, for example), or a two-dimensional arrangement, or a multi-dimensional arrangement. (In practice, it is difficult to deal geographically with arrangements beyond three dimensions.) In a uni-dimensional ordination, the information will be arranged to show its sequential structure, the most dissimilar information being furthest apart. Thus, a simple geographical transect will have the ends of the axis determined by distance apart. A gradient ordination may take a factor such as pH range, with the ends determined by the extreme environmental range of pH in the samples, and species distribution placed on this axis according to their relation in the samples to this factor. In a two-dimensional ordination, a second axis may be used, placed at right angles to the first, based on a difference significant in relation to both axes. The process can go on with further axes.

More abstract ordination methods are designed to extract one or a few axes, arranged to reflect the vegetational composition of samples with as little distortion as possible. The *Wisconsin comparative ordination* uses two dissimilar samples to form the end points of an

axis, and samples are arranged along it according to the degree of similarity to the two ends. The samples with the greatest dissimilarity in the medial range of the order may then be used as end points of a second axis, and the samples repositioned to yield an ordination in two dimensions. This technique should be distinguished from that of *principal components analysis*, which is yet more abstract. Figure 7.8 shows an example of this technique. Unusually, the samples in this example are physiognomic and the axes are environmental variables.

Modern phytosociology now has an 'embarrassment of techniques' for the collection and analysis of data. However, these techniques alone do not give answers to the fundamental questions of plant ecology. As McIntosh (1978) has pointed out, there still remain the problems of first assessing the techniques, and secondly relating the results of such techniques to the environment so that 'causal relations between vegetation and the physiological and population responses may be elucidated'. (For a comprehensive exploration of the nuances
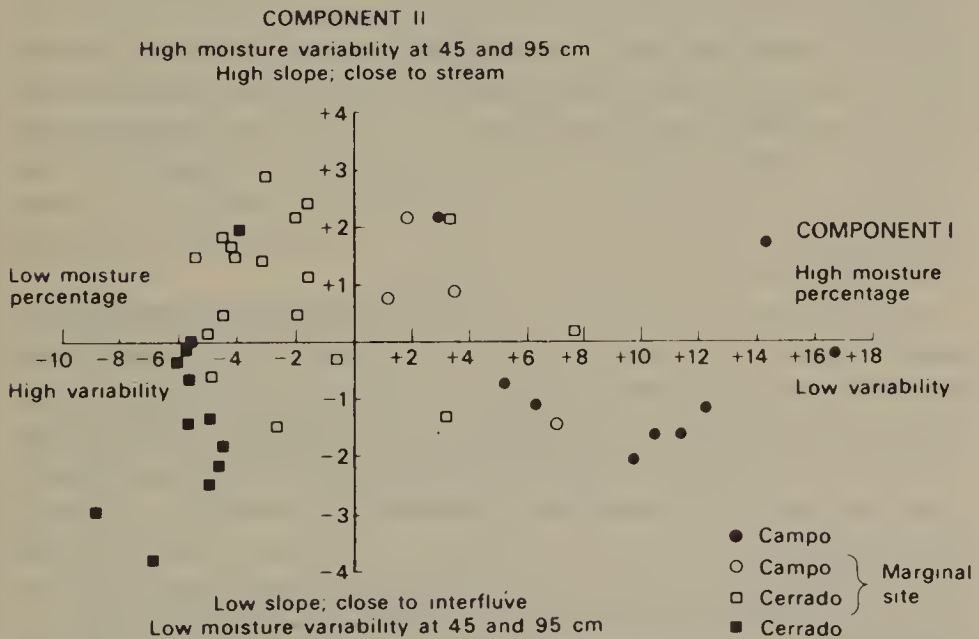
Figure 7.8 An example of a mathematical ordination technique (principal components analysis). In this example, 12 environmental variables from 43 monthly-sampled sites in the northeastern Matto Grosso have been distributed to the two axes, components I and II. These axes describe an ellipsoid scatter of points, each point representing a correlation between the variates studied. It can be noted in this example how the component analysis of the correlation matrix has differentiated significantly between the largely grassy vegetation (campo) and woody scrub vegetation (cerrado). (After Daultrey (1970).)

of phytosociological methodologies, see Prentice and van der Maarel (1987).)

7.5   The mapping of plant communities

Reflecting the variety of ideas as to how vegetation should be analysed and classified is the variety of ways in which it may be mapped. There is no single map of vegetation that can represent all the information relevant to its character or can satisfy all the needs for information about it. This has been neatly demonstrated by tests devised by Küchler (1956) of mapping methods over the same piece of ground. Taking the varied needs of a soil scientist, a geographer in an underdeveloped country, an animal ecologist, a commercial beekeeper, a military strategist and a tax assessor (it is surprising just who needs to know about plant geography!), it was quite clear that the vegetation map that best fulfilled the needs of each would require a different scale, method of representation and classification.

Although the diversity of needs for information about vegetation is very wide most published maps result from the particular methods and needs of botanists, geographers and ecologists, and tend to reflect the priorities of each discipline. Thus, most maps may be described as physiognomic, floristic, regional or ecological, and may be drawn on small, medium or large scales. No matter into which category they fall, they all rely critically on the sensitivity and internal fidelity of the classification system adopted.

From the 19th century down to the present day, physiognomic maps, because of their utility for a variety of purposes, have constantly been published. On the whole, their relative simplicity makes them particularly suitable for land planning, forestry, conservation, agriculture, military planning and these days for rapid aerial survey. They have been published on a variety of scales, although the use of medium scales is rare as it tends to make the maps too small for synthesis and too large to remain sufficiently accurate. Notable examples of physiognomic maps include that of the USA by Küchler, those by Gaussen in the *Atlas de France* and many others in the various great world atlases.

In France, the vegetation map has become a subtle and informative document carrying the maximum useful information about plant communities and their ecology. There are two main centres for production of these maps. One, at Montpellier, produces maps for the purposes of scientific research into the problems of vegetation,

and these are usually of specified critical areas at a scale of 1 : 20000 or larger. The production of these maps is integral to the work of a scientific institute, the Centre d'Études Phytosociologiques et Écologiques, which carries out field survey, classification and experimental investigation of the problems of vegetation. The other main centre, the Service de la Carte de la Végétation de la France at Toulouse, is concerned with publishing maps of more general use at a scale of 1 : 200000 based on the methods developed by H. Gaussen. These maps are much more empirical in scope and include information about environmental conditions as well as natural and agricultural vegetation, and have additional inset maps at 1 : 1250000 showing aerial coverage, administrative boundaries, land use, climax vegetation, soils, agricultural hazards and annual means of temperature and precipitation. There is also a wealth of marginal textual information. Altogether, the beautiful and subtle colour printing and layout make these a triumph of the cartographer's art and the maps are superb regional geographies in themselves. Deservedly they have become central documents in the planning process in France. The Toulouse centre has taken on the formidable task of mapping world vegetation at a scale of 1 : 1000000, and although this has meant a reduction in the number of colours and symbols, the maps, together with their inset and marginal information, are nevertheless indispensable to the modern study of world biogeography.

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PART 2

The vegetation of tropical and temperate regions

8

Vegetation and climate: an introduction to world vegetation patterns

One of the most difficult problems in ecology and biogeography is the correlation between vegetation and climate. The workers who laid the foundations of plant geography assumed that, viewed on a large scale, the major vegetation unit (formation-type) represented the response of the plant kingdom to a major climatic type. Thus, for each climatic division recognized by the climatologists, there should be an appropriate vegetation type. However, the vegetational anomalies that occur in broadly similar climatic types around the world are so numerous that, as one worker has said, 'It is pointless if not positively misleading to make generalisations about such relationships' (Eyre 1968 p. 182).

Yet, as we have seen (Fig. 6.1), the plant–soil system *is* limited by the atmospheric system, so it would be equally erroneous to suggest that there is no correlation at all. That vegetation varies 'in tune with climate on a continental scale' (Walter 1984) is undeniable. In trying to establish the notation of this tune, there are three main aspects to the problem:

(a) the nature of climate itself, i.e. what exactly it is that we measure, and what is its biological significance;
(b) the fact that each species makes its own response to climate within the framework of its genetic inheritance; and
(c) the fact that the relations of vegetation to climate seem to be more than simply the sum of these individual responses.

Standard meteorological returns on which climatologists base their climatic definitions lack essential data of biological significance, especially the all-important potential evapotranspiration (PE) figure,

and it has not really been proved that this figure can be adequately derived from standard data. The best-known attempt is that of Thornthwaite (see Hare 1954) and there is some evidence that the PE climatic types defined by his methods can be loosely correlated with vegetation variations (Fig. 8.1). However, in the tropical world the index seems altogether too coarse to relate to vegetational variation (Whitmore 1975). The method established by Penman (Sec. 4.4) relies, in any case, on data not available from standard returns, and its usefulness in relation to tropical vegetation is uncertain.

Even if it were possible to establish unequivocally a reliable index for PE, this would still not necessarily tell us about moisture availability to plants; there is also the factor of soil to consider. As Figure 6.1 makes clear, moisture is usually only available through the soil. In any two habitats with the same PE index but with soils of differing porosity and field capacity, the water relations of plants may be widely divergent. For example, a Royal Society–Royal Geographical Society expedition to the Brazilian Matto Grosso found that there were sharp boundaries between savanna and dry forest in the expedition's study area, with few characteristics of continuous change across these (Askew *et al.* 1970–71). The change coincided with a striking disparity in soil texture between the two vegetational types,
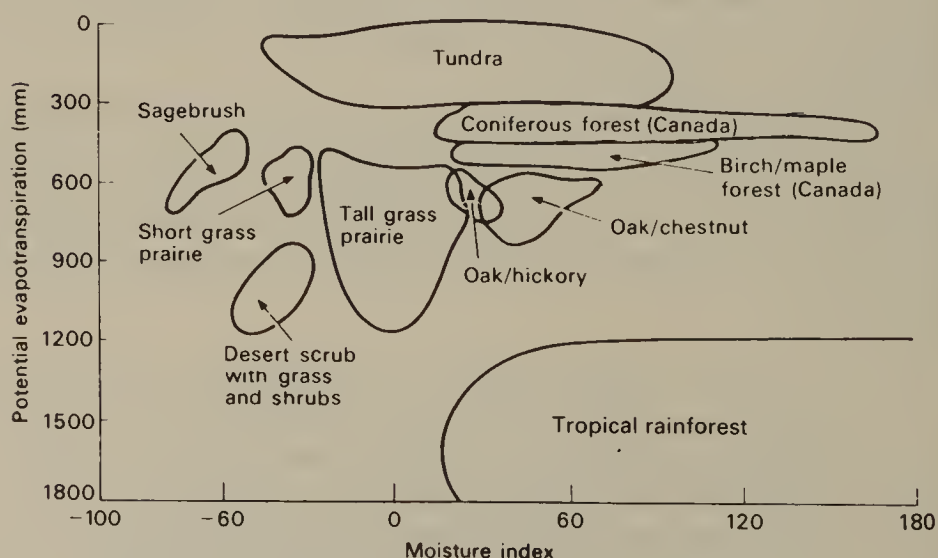
Figure 8.1 Relation between climatic moisture index, potential evapotranspiration and natural vegetation. The areas enclose values from many observation sites and the natural vegetation at these sites is indicated. Note that the moisture index is given by S/PE, where S is the annual water surplus and PE the potential evapotranspiration. (After Mather and Yoshioka (1968). © Association of American Geographers.)

and the hypothesis is that this change and its effect on moisture availability operate to tip the balance between the two vegetation types at a critical point on the moisture gradient.

A further difficulty in establishing the bioclimate is that of fire. This vital habitat factor is not easily quantified and, as we saw above (Sec. 5.6), its occurrence need not be frequent to produce important effects in vegetation.

A telling illustration of the complexity of species response to the climatic environment has been provided by the work of Pigott (1971) on the stemless ground thistle (*Cirsium acaulon*). It has been clearly shown that the failure of this plant to produce fertile fruit near the northern limit of its range in Britain is controlled by the complex interaction of *all* the elements of climate with which its distribution can be correlated. These elements – daily maximum temperatures, duration of sunshine and rainfall during the summer months – act in concert to affect the physiology of this species' reproduction. Nor are the biotic effects of attack by slugs and fungus on its fruits by any means negligible factors in its inability to spread. As Pigott rightly points out, the neglect of the complexity of plant response to the equally complex variables that constitute climate is 'not easily excused'.

Where plants are aggregated together to compose a vegetation cover, a third variable is introduced. Many of the aspects of climate are profoundy influenced by the vegetation itself: windspeed, temperature, exposure of the ground to direct insolation, evapotranspiration and so on. Although Gleason has convincingly argued the principles of species individuality, no species has, in fact, evolved in isolation from others. In relation to light, for example, there are few species that are indifferent to the shade cast by other plants. Plants of closed forests can usually only spread with the spread of forest. In the tropical lands, rainforest **epiphyte** species have evolved to take advantage of the microclimate within the tree crowns, and so on.

Finally, there is the whole question of human activities as a factor affecting climate. Where clearance and/or burning have occurred, the microclimatic environment may be drastically altered. Thus the ground thistle is usually found in calcareous pastures, which, to a large extent, are an artifact of farming systems. The habitat conditions, climatic and otherwise, would have been radically different for this species before any clearance took place.

Because of this kind of uncertainty, many texts on vegetation geography contain 'poorly founded conclusions as to causation' (Pigott 1971). In truth, we really know very little about the ways in

which climate operates to limit the distributions of (a) individual species and (b) individual vegetation types.

As Pigott and others have shown, the interactions of plant life-cycle, life-form, species demography and habitat, and biotic influences at the edge of its geographical range are very complex. Nor can the random perturbations induced by climatic change in both recent and geological time be ignored. As Chapter 2 makes clear, much of the world's vegetation, in middle and high latitudes, especially, but also significantly in low latitudes, has undergone striking changes of distribution during the Quaternary. Moreover, work by historical climatologists, for example at the University of East Anglia, has revealed quite marked short-term climatic variability. The so-called 'Little Ice Age' from the late 17th century to the end of the 19th century seems to have involved some changes in vegetational pattern in high latitudes. However, once ecosystem types are solidly established on land surfaces, 'vegetational inertia' (Sec. 2.5) becomes an important factor in the maintenance of geographical pattern. (See the work of Neilson below.)

Two examples may illustrate these points, both drawn from the vegetation of the USA.

The first questions whether the distributions that we now observe can be related to contemporary macroclimate patterns in mid-latitudes at all. We have already seen that 'vegetational inertia' of species can occur, but in this case the problem raised is one of migration rates in response to climate. Brown and Gersmehl (1985) established theoretical migration models for six grass species of the American mid-continent and compared these with actual distribution. In nearly all cases the model's predictions of the areas these grasses should occupy at this stage in postglacial history did not match their actual distribution. The authors conclude that the Plains grasses are, even at this remove from Quaternary glacial conditions, not yet in equilibrium with their environment. Indeed, some species appear still to be actively migrating in delayed response to postglacial climatic change.

The second example employs the findings of what has been called the 'new meteorology'. Through a combination of the kind of historical climatic studies mentioned above and the study of recent atmospheric and oceanic anomalies, such as those which have afflicted the northern Trade Wind belt in Africa. India and western South America (Ramage 1986, Glantz 1987, Meehl 1987), a general consensus amongst atmospheric physicists, climatologists and oceanographers has developed in recent years. This holds that these

longer- and shorter-term climatic fluctuations are generated by particular variations in the fluid dynamics of the linked atmospheric and oceanic flow structure.

The basic nature of the flow structure of the atmosphere and oceans is determined primarily by the temperature gradient from low latitudes to polar regions and secondarily by the effect on the moving air and water masses of the Coriolis force produced by the Earth's spin. The dynamic pattern that results contains within it semi-permanent atmospheric and oceanic features, for example the Hadley cells, the polar high-pressure cells, the intertropical front or convergence zone, oceanic currents and the mid-latitude jet streams. These features are subject to both longer and shorter disturbances, and it is the understanding of the association (termed 'teleconnection') of these variations with climatic anomalies that has led atmospheric physicists to present relatively comprehensive explanatory models. For example, the mid-latitude jet streams do not circulate smoothly from west to east around the Earth but contain waves, the so-called Rossby waves, along which the jet stream swings alternately north and south. At times when the poleward temperature gradient is very marked, for example during a Quaternary glacial episode or when there is an overall cooling period in the Earth's climate, the Rossby waves tend to become fixed as deep, meridional, standing waves resonating to the pattern of distribution of land, sea and mountain ranges. At other times when there is a warming trend or during an interglacial epoch, the north–south amplitude of the Rossby waves decreases, and the wavetrain circulates more zonally from west to east. As the surface air masses and their detailed interaction in weather patterns are controlled by the Rossby waves, clearly the behaviour and position of these waves is of critical importance as an explanation of shorter- and longer-term climatic trends.

Neilson (1986) has applied these insights to the vegetational biogeography of southern New Mexico, with considerable success. As he points out, although there is general agreement amongst ecologists that vegetational distribution on the macroscale is climatically determined, the lack of an adequate climatic model has led many (if not most, cf. Eyre (1968) above) biogeographers either to ignore climatic variations at a detailed level altogether or to treat them merely as background. He argues that this need not nor should not be the case and that the application of the 'new meteorology' can provide comprehensive explanatory models for vegetational distributions even at local levels as exemplified by the vegetation of New Mexico.

As a starting point for this work, Neilson takes the finding that during the last 100 years or so there have been three distinct climatic regimes: two (before 1900 – the end of the 'Little Ice Age' – and post-1940) had a predominantly meridional flow associated with a cooling trend and the other (1900–40) a general warming trend and zonal flow. As geographical expansion and contraction of species' range are dependent on the process of dispersal of propagules and the opportunity to complete life-cycles successfully, then (a) there should be clear indications in the patterns of vegetation of the effect of decades of particular weather types on these processes and (b) by close study of minor variations in recent weather ('high-resolution climatic analysis') and their effects on plants, it should be possible to establish plausible causative links between global climatic trends, weather types, life-cycle variation and distribution patterns.

In a detailed analysis of the weather patterns in the Las Crucas area, Neilson (1986) identifies warming and cooling weather patterns during the last 100 years and the concomitant liability to summer or winter droughts. The hypothesis is advanced from this that the particular period of drought, whether summer or winter, has differential effects in relation to the particular photosynthetic pathway type of semi-desert grasses and shrubs. The former have C3 pathways that respond well to late summer rainfall, the latter C4 pathways that respond well to winter rainfall (see Section 13.1 for an account of C4 and C3 photosynthesis). By carefully matching short intervals of weather in recent decades which mimic the climate of warming and cooling periods and correlating these with seed production and life-cycles of grasses and semi-desert shrubs, Neilson demonstrates that the mosaic vegetation pattern of grassland, shrubland and former juniper forest can be ascribed to a combination of (a) warming and cooling spells in the postglacial period, which favoured one or another vegetation type sufficiently that territory could be expanded, and (b) vegetational inertia, which preserved sufficient of the territorial area to maintain a particular vegetation type and carry it through less favourable spells.

In this work Neilson has clearly demonstrated and brought firmly to the centre of vegetational and ecological study the climatic hypothesis, which as we saw in Chapter 1 formed the primary basis of vegetational biogeography. Although Eyre (1968) may be correct that anomalies are very frequent, Neilson has shown that these need not vitiate the climatic hypothesis now that there are sufficient data to apply historical climatology as an explanation.

By and large, however, for most parts of the world, biogeographers

will still have to rely on the adaptation of generalized climatic data such as those developed by Walter and Lieth (1969), Holdridge (1947) and Sewell (1985). The first has been widely used to correlate **zonal vegetational types** on a continental scale, the Holdridge life-zone system much less so.

Walter and Lieth (1969) present more than 8000 ecological climate diagrams from stations all round the world which show not only the temperature and precipitation but also the length and intensity of relatively humid and arid seasons and the liability to early or late frost. By using the scale of $10°C = 20$ mm of precipitation, the diagrams allow an idea of potential evapotranspiration to be obtained for most stations except steppe areas where the scale of $10°C = 30$ mm of precipitation is used. (For a straightforward introduction to ecological climate diagrams see Walter (1984).)

Sewell (1985) has developed a predictive model using relatively easily obtained climatic data, for example mean monthly temperature and mean monthly precipitation. Employing data from 176 North American stations with 30 additional randomly selected stations to test the model, predictions of expected vegetation formation at the location of any particular station are generated from the generally agreed climatic associations of particular vegetation types. The results correctly predicted the vegetation for 87% of the locations. Sewell suggests that the anomalous results could be useful in pin-pointing areas where non-climatic, eco-geographical factors are especially important.

It may be concluded from the foregoing that no single climate–vegetation model exists that can produce comprehensive causative explanations for the geographical distribution of vegetation types, although it is generally agreed that climate is undoubtedly the prime explanation for the pattern of the world's vegetational biogeography (Grace 1987). Once established on a land surface, many of the species that compose the major vegetation types can resist often quite dramatic changes in climate, as the phenomenon of vegetational inertia demonstrates. In this process, it is very often edaphic factors especially that can work to favour established plants by vitiating the competitive advantage of species more suitable to the prevailing climate.

Some of the difficulties noted above stem from the contrasting approaches of the ecologist and the geographer. Ecologists are concerned with precise field and experimental evidence on which to construct hypotheses to explain the observed facts; geographers tend to deal in the generalization of very complex phenomena in order to

discern the links by which various natural and human patterns on the Earth's surface interact to produce its varied characteristics. In historical terms, it was the approach of the geographer that dominated the view of world vegetation until comparatively recent times. As ecological research has proceeded, one of the most striking facts to emerge about generalized vegetation categories has been the diversity of ecosystem structure they conceal beneath their apparent uniformity. In one case after another the generalized categories of the geographers – savanna, temperate deciduous forest, tropical rainforest, etc. – dissolve to reveal intricate mosaics of minor

Figure 8.2 Generalized distribution of the world's vegetation types (from various sources): (1) tropical rainforest; (2) tropical seasonal forest of various kinds; (3) savannas (classified in various vegetation maps into many subcategories, e.g. thorn forest, thorn woodland and scrub, broad-leaved tree savanna, etc.); (4) forest of warm and cool temperate affinities including deciduous summer forest (Ds), evergreen mixed forest (Ev), broad-leaved evergreen forest (Bl), eucalyptus forest (Eu) and southern pine forest of USA; (5) mixed boreal and deciduous forest of the Northern Hemisphere; (6) boreal forest (also including west-coast forest of USA); (7) temperate grasslands; (8) vegetation of arid and semi-arid lands (highly variable, including cactus scrub, thorn scrub and many woody and sparse grass formations); (9) tundra; (10) mangrove coasts; (11) true desert with intermittent plant cover; (12) montane vegetation of the Andes and Abyssinian highlands, which includes major formations of tropical montane forest; (13) alpine vegetation of central Asia with extensive grassland areas; (14) Wallace's line, in south-east Asia.

ecosystems loosely contained in the overall framework determined by the macroclimatic characteristics.

Some of this mosaic pattern may be due to palaeoecological events, especially Quaternary climatic changes, and some to the activities of man, but some appear to be inherent in the ecosystems themselves. Now we shall look at the ways in which these and other factors dealt with in Part 1 interact to produce the pattern of the world's vegetation. This distribution of vegetation types is summarised in Figure 8.2.

In addition, we shall give some account of the relationships that human beings have established with the soils and vegetation of the major ecosystem types. In a book of this scope, the appraisal will perforce be brief, but for authoritative analytic updates on environmental and development problems, the reader is rcommended to consult the annual report from the Worldwatch Institute (e.g. Brown *et al.* 1987).

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9

Tropical forests

With the advent of remote-sensing techniques, estimates of the land surface of the world occupied by tropical moist forests have generally been revised upwards from earlier estimates. Estimates of biomass, however, have generally been revised downwards from earlier figures. Figures using data from Lanly (1982) prepared for the FAO suggest that the total extent is around 1081×10^6 ha, which represents about 65% of its original extent prior to the Neolithic farming 'revolution'. The more recent figures are generally higher than those accepted earlier, but there is no disagreement that these forests represent the most species-rich environments on Earth, containing between 20% and 40% of all the world's plant and animal species (Myers 1983). Although understanding of tropical rainforests has increased in the last three decades and a number of major studies have been published (Golley 1983, Leigh *et al.* 1983, Sutton *et al.* 1983), there are still major areas of disagreement on fundamental aspects of the ecology. This is not surprising as they represent the most complex biocoenosis that life has evolved, with a high order of dynamic organization and many unique features of morphology, life-history and community interaction.

9.1   Rainforests: structural characteristics and areal variations

The life-form groups that comprise the forest have been analysed by Richards (1952) as follows:

(a)   **autotrophs** (i.e. with chlorophyll)

   (i)   mechanically independent plants – trees, treelets and herbs;
   (ii)   mechanically dependent plants – climbers, stranglers and parasitic and non-parasitic epiphytes.

(b)   **heterotrophs** (i.e. without chlorophyll)

(i)   saprophytes – particularly fungi;
(ii) parasites – particularly fungi.

Each of the groups (i) and (ii) represents a partial life-form community (or **synusia**) within the forest. In any tract of forest the proportions of these synusiae will vary according to the *phase* of forest development. It is conventional to recognize three main phases of forest development: gap phase, building phase and mature phase (Whitmore 1975). Although regeneration from the gap to the mature phase is continuous, the three phrases can usually be identified in the forest physiognomy. The gap phase would be defined by seedling trees not exceeding 2.7 m and saplings less than 0.3 m girth, the building phase by pole-sized young trees (0.3–0.9 m girth), and the mature phase by full-sized trees. Thus the areal pattern of these forests is a mosaic of forest patches (Fig. 3.7) at all stages from gap to mature. The species composition of these mosaics is usually highly varied, and gregarious dominant species are rare. Over large tracts of lowland forest the canopy will be composed of tree species not contributing more than 1% to the total number of species. Family dominance, however, is more common. For example, in the lowlands of Malaya, the Dipterocarpaceae may be said to be dominant (Whitmore 1975), although in these still-complex forests this dominance may be expressed by no more than the fact that the Dipterocarpaceae provide perhaps 25% of all mature tree species. This is in marked contrast to parts of Borneo, where the dominant large dipterocarps may provide 90% of all the emergent big trees. In the American tropical rainforests, single dominance is expressed especially by the legumes. (*Epurua falcata* and *Mora* spp.), which may often form single-dominant stands on poorer soils. In Africa, single-species dominance is associated with another legume (*Gilbertiodendron dewevrei*), again on unfavourable soils.

The areal pattern of tropical rainforest is also varied by the differing formations it encompasses. Some of these are shown schematically in Figure 9.1. As can be seen, differentiation into distinct formations also partially serves to differentiate the climatic and soil factors that influence their occurrence and distribution.

Floristically the four main regions (American, African, Indo-Malaysian and Australasian) of tropical rainforests are quite distinct and there are only a few woody pantropical species and genera. Other non-tree plants, especially the epiphytes, are also regionally distinctive. Thus, in Indo-Malaysia the epiphytic synusia is dominated by the orchids, ferns, Asclepiadaceae and Rubiaceae. In
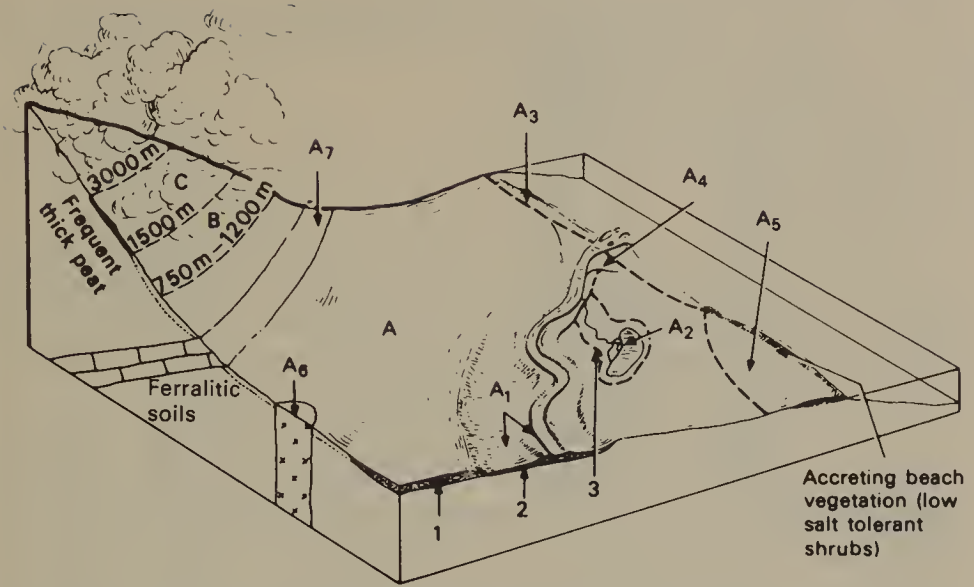
Figure 9.1 Formations within tropical evergreen rainforest vegetation type. (Formation nomenclature from Whitmore (1975). (A) Tropical lowland evergreen rainforest: A_1, freshwater swamp forest; A_2, peat swamp forest (extensive in Sumatra); A_3, mangrove forest; A_4, brackish-water forest; A_5, heath forest over sands; A_6, forest over ultrabasic rocks (occasional in South-East Asia); A_7, forest over limestone (rare in Africa). (B) Tropical lower montane rainforest. (C) Tropical upper montane rainforest. The numbers 1, 2 and 3 are common in Amazonian usage: (1) 'terra firma' with mesic forest; (2) 'várzea forest' liable to inundation by 'white river' water; (3) 'igapo forest' liable to inundation by 'black river' water. Alternative terms used by FAO classification: (A) tropical ombrophilous forest (lowland type); (B) tropical ombrophilous mountain forest; (C) tropical ombrophilous cloud forest.

America, in addition to orchids and ferns, the bromeliads and cacti are important (see Longman and Jenik 1974 p. 71). Moreover, within each of the major regions the floristic composition of the various formations alters gradually through space. In Indo-Malaysia, for example, the forest cover of the lands bordering the Sunda continental shelf has a rich dipterocarp flora (10 genera, 350 species) with many endemics, but northwards and eastwards this rapidly becomes impoverished.

The vertical structure of the forest has been described and drawn by many authors, usually by profile diagrams (Fig. 9.2). But even now there is still some uncertainty as to whether or not the rainforest exhibits layering into identifiable strata as do the temperate forests. In one view there are – or should be – five recognizable above-ground strata:

(a) upper tree layer, above 25 m (emergent trees with woody climbers and epiphytes);
(b) middle tree layer, 10–25 m;
(c) lower tree layer, 5–10 m;
(d) shrub layer;
(e) herb layer.

Root layers reach down further into the soil than was previously commonly understood. From 21 to 47% of roots are in the first 10 cm, the rest mostly in the next 20 cm, but 5–6% of roots extend below this as far as 2.5 m below the surface (Huttel 1975).

Whether specific plant associations occur related to generalized niches or whether the rainforest is a haphazardly varying, single, unified community is also still undecided. Probably the answer lies somewhere between these two views (Whitmore 1975). Discrete associations can certainly be identified. Most of the variation between these may be ascribed to a complex of factors including availability of flora, variation of topography and soil type, 'reproductive pressure' (i.e. in certain circumstances, a variety of factors give advantage to some species) and minor soil differences in uniform topographic types.

These varying factors and their influence on vegetational composition have been demonstrated in Australian rainforests. Beadle (1981) has presented 18 lists of forest stands in which these are revealed. Some 818 species reach over 45 cm in height, of which 269 species were trees. Computer analysis revealed six floristic groups in the 18 lists, with three stands in each group. Further study, extended over 20 degrees of latitude, showed that the combinations in which the species occurred were constantly changing. Newberry *et al.* (1986) have also discovered in the forests of Sarawak (Borneo) that tree species in these dipterocarp forests can be differentiated into those with a tendency to form clumps, and those with little tendency to display clumping. The difference here seems to arise from the ecological behaviour of the two sets of trees. In the first case, the species are more light-demanding and tend to grow rapidly from the soil seed bank in substantial gaps produced by windthrow. The latter, on the other hand, are shade-tolerant and slow-growing, remaining for long periods as saplings, which eventually reach the canopy when single tree gaps appear.

One model that has been much discussed attempts a general explanation of the noted species richness of these forests. This is the so-called Janzen–Connell hypothesis (Connell 1970, Janzen 1970).
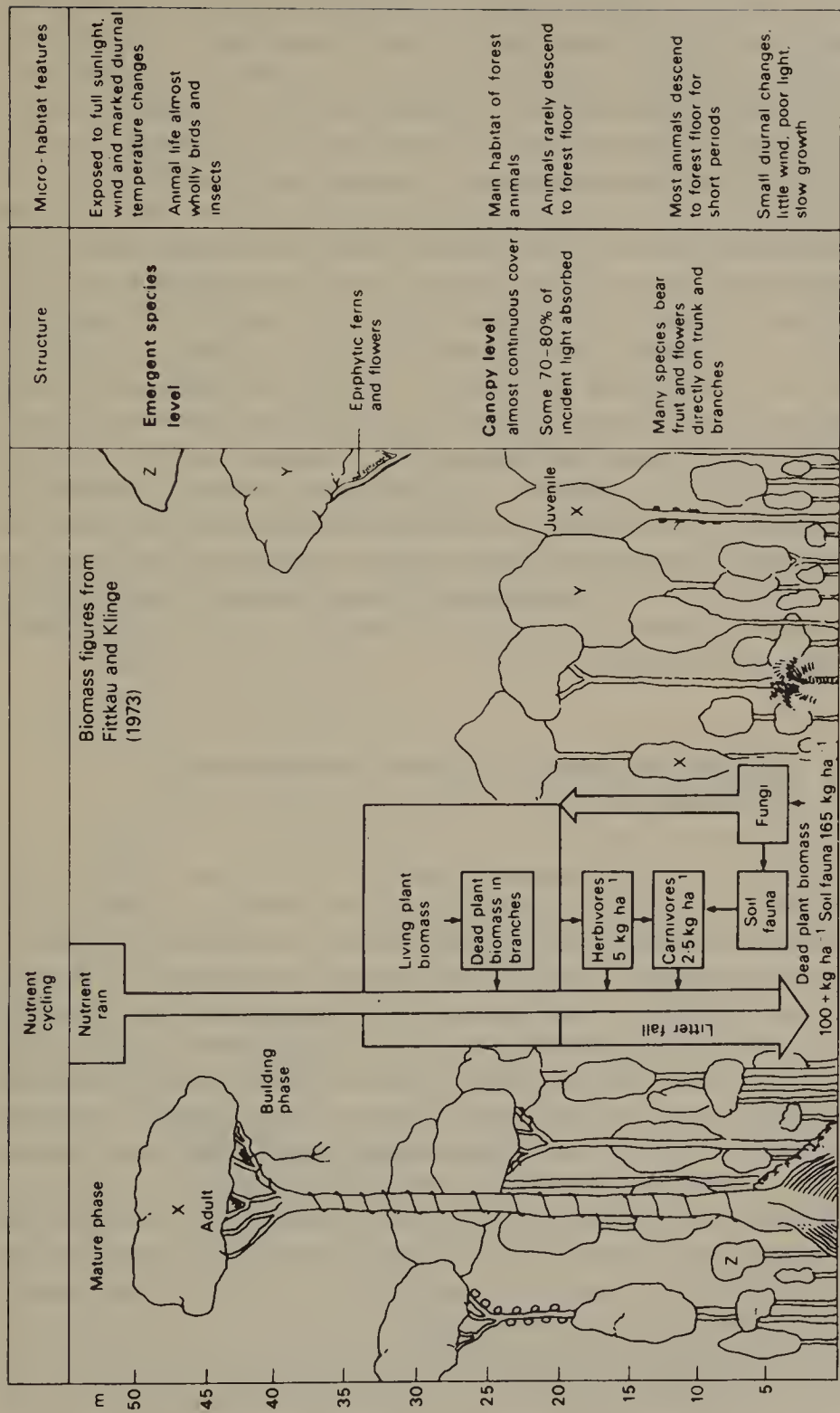
Figure 9.2 Tropical lowland evergreen rainforest. (Composite profile adapted from examples in Richards (1952) and Whitmore (1975).)

The model was simultaneously but independently put forward by these authors, and suggests that the key to understanding species distribution lies not solely in their reproductive capacity but especially in their mortality patterns. It is suggested that the death of individual plants has an important spatial component. The general effect of mortality from whatever cause, the authors hypothesize, will tend to result in the mature trees of some species at least being evenly distributed. However, the hypothesis has not yet been proven, as many studies show trees are rarely, if ever, evenly distributed and clustering of species is a common feature, although at least one study (Sterner *et al.* 1986) provides limited support when post-germination survival of individuals is carefully mapped. This same work itself suggests a general spatial relationship for tropical forest trees, based on 'repulsion' between individuals of the same species. This repulsion may result from a number of causes: seed predators, herbivores, interference competition, exploitative competition and physical crowding. As the authors point out, most of these factors are to do with feeding and therefore suggest that biotic–trophic relationships may be very important in the spatial dynamics of tropical rainforest species distributions.

9.2   Rainforests: climatic and other environmental relationships

Generally, the most important climatic characteristic to which the distribution of tropical rainforests can be related is rainfall. It is, however, quite impossible to give other than rather vague figures – more than 2000 mm mean annual rainfall, for example – as to how much rainfall is necessary before a rainforest vegetation can develop. As we saw above (Ch. 4), water supply to a plant depends on a number of variables, especially the balance between precipitation and evaporation. This is dependent in turn on topography, soil type, runoff and so on. To describe the tropical rainforest climate as hot and wet, with the assumption that precipitation always exceeds evaporation, is an oversimplification. Although various attempts have been made specifically to design climatic extrapolations from standard data for rainforests (see Whitmore 1975 pp. 43–51), none has been entirely successful. Important features of biological significance may be lost in the generalization.

For example, over the last few decades detailed studies of the hot, wet forests have revealed surprising variations within the generalized

climatic type. Thus, in South-East Asia annual periods of soil moisture deficit have been observed throughout the Malay Peninsula apart from its southern tip and similar observations have been made elsewhere. Even at or near the equator soil moisture deficits have been recorded. In the Congo Basin, for example, the soil moisture has been observed to fall below permanent wilting percentage for the whole of the month of August (Longman and Jenik 1974 p. 35). These brief periods of moisture stress, seasonal or otherwise, have been recognized as important correlatives of flowering time in many species (Brunig 1971).

Other important bioclimatic features hidden in the average figures include the observations that:

(a) moisture deficits are recorded more frequently at coastal stations than at inland stations;

(b) soil depth plays an important part in determining whether plants will suffer moisture deficit or not – in general, the deeper the soil the less chance of stress;

(c) the forest itself serves to control evaporation rates, which have been observed to be less from open evaporation pans than from the vegetation;

(d) dry, sunny spells have effects on growth periodicity and may increase or decrease forest productivity according to site conditions – sites with abundant nutrients produce significant growth, and oligotrophic sites may decrease growth (Brunig 1971).

Rainforest plants must be adapted not only to these intermittent climatic variations but to the wide variation of diurnal climate inherent in the forest structure. Thus, the plants of the forest are not hygrophytes but are generally mesophytes. Within the forest structure, the response to the vertical differentiation of microclimate can be most easily observed in the leaves. On the whole the bigger, emergent trees have smaller leaves than those lower in the structure. Furthermore, the positioning of the leaves in the leaf mosaic of most trees seems to be a compromise between photosynthetic needs and the avoidance of moisture stress (see Sec. 5.6 on canopy shape). Indeed, in some species of emergents, for example *Piptadeniastrum africanum*, leaves markedly alter their positions in relation to the Sun during the day, the movement being controlled by specialized *pulvini* (leaf joints). The overall architectural form of trees has also been shown to play a significant part in the forest structure, especially in

relation to successional status of individual species (Hallé *et al.* 1978, Shukla & Ramakrishnan 1986).

The height that the forest reaches therefore depends on a number of variables – moisture availability, site conditions, any dry season, etc. – which determine the net production that can be sustained. Figure 9.3 illustrates the gradient of forest height observed through a transition between vegetation types in South America. It can be seen that the greatest heights obtain in intermediate conditions. Where rainfall is excessive (mean annual total above 3500 mm), leaching of soil nutrients and reduced radiant energy due to cloud may significantly reduce forest production. In the Amazon Basin along the Rio Negro, low, open stands (Amazonian caatingas) occur in these conditions. Most rainforest emergents on mesotrophic sites can reach 50 m and in the most favourable conditions on eutrophic soils (for example, the upper parts of floodplains) the most luxuriant stands
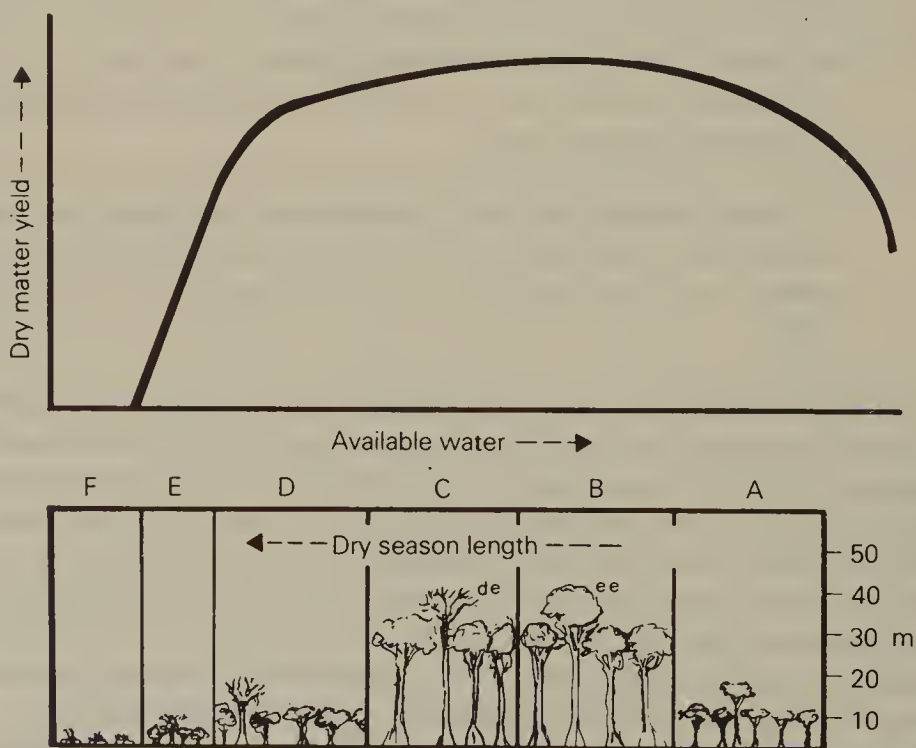
Figure 9.3   Relationship of yield, water availability and forest types. (Based on data from Brunig (1971).) (A) Amazonian caatingas. (B) Tropical lowland evergreen rainforest. (C) Tropical evergreen seasonal forest. (D) Tree savanna/seasonal forest ecotone. (E) Tree savanna. (F) Desert scrub. Note that canopy heights shown are not the general rule for all tropical forests, e.g. in South-East Asia (B) would be generally higher in dipterocarp forests.

exceed 60 m. In general, forest with some seasonal drought is higher than continuously wet forest (Longman and Jenik 1974).

Many rainforest plants also show a clear response in growth rate to quite small temperature changes (in some cases 1°C or less). As the diurnal range of temperature at the emergent level can exceed 10°C and even at ground level may be more than 1°C, temperature change, however apparently insignificant, is an extremely important biological factor.

Growth in tropical rainforest species is not continuous. There is usually a definite period of shoot elongation, which can be surprisingly short (in rubber and mango, two weeks or less), and in many species a definite seasonality can be observed, with the main peak of growth just after the 'dry' season (Medway 1972), as shown in Figure 9.4. The controls of growth rhythm and leaf 'flushing' appear to be very complex, however. In some species they seem to be a function of an internal 'biological clock', in others a response to variation in the external environment. One remarkable but little understood feature of leaf production is the spectacular colour of newly flushed leaves, which may be pink, red or even blue.

9.3   Biomass, production and mineral cycling in rainforests

It has gradually been realized that, although these forests are luxuriant, the evidence that they are therefore highly productive is not strong. More and more studies have revealed that earlier estimates of production were too high. For example, a forest studied in the Ivory Coast showed a gross production of 52.5 t $ha^{-1}y^{-1}$, but at least 75% of this was lost by respiration. This compares with gross production figures from central European beechwoods of around 23.5 t $ha^{-1} y^{-1}$, with respiration losses of only 43%. Thus, the values for net primary production of the two forests are approximately equal (13.4 t $ha^{-1} y^{-1}$ for tropical rainforest and 13.5 t $ha^{-1} y^{-1}$ for beech forest). A number of authors (Proctor 1983, Jordan 1985) have pointed out the discrepancy and have also demonstrated the difficulties in obtaining accurate measurements. Lieberman (1982), for example, found that girth increase in trees was so slow that it may take years for the increment in thickness to exceed background fluctuations produced by the variation in weather from year to year. In a 14-month study of trees of several species in Ghanaian forest, he found that the girth of some of his specimens was actually *reduced* in thickness over the period.
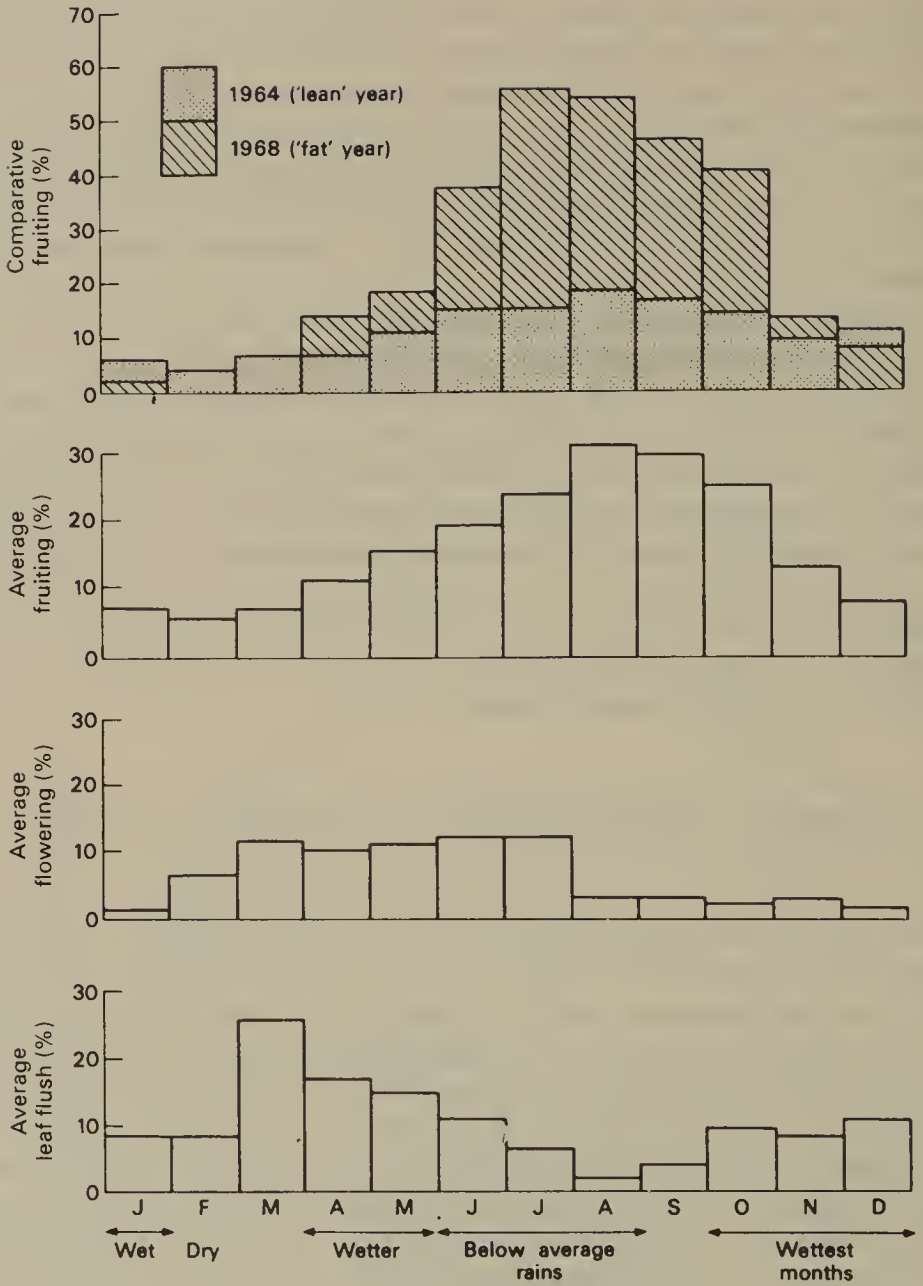
Figure 9.4 Seasonality in tropical rainforests. (Data from Medway (1972) based on Ulu Gombak forest, Malaya.) Note the distinct relation of physiological activity to seasonal rainfall regime. Seasonal incidence of breeding (peak: March, April, May) and moulting (peak: August, September, October) in insectivorous birds are also related to the above rhythm, as are variations from year to year of breeding success ('fat' years – high breeding success; 'lean' years – low breeding success). The top diagram compares the percentage of 58 trees in fruit in two years. The other three diagrams show averages for 58 trees over the period 1963–69.

One of the major reasons for the frequent overestimate of the production rates in these forests is the massive litterfall that is a constant feature of the forests. Fittkau and Klinge (1973), for example, found in their study area, in the central Amazonian rainforests, a total annual litterfall of $11 \, t \, ha^{-1}$. Soil nutrient reserves are usually small, however, except in lowland peat-bog forests and upper montane forest areas. In general, in the wet, tropical lands, litter is destroyed faster than it is supplied where mean temperatures are above 30°C (Fig. 9.5). Between 25 and 30°C litter decomposition and supply are about equal. Humus turnover is about 1% per day, so there is little chance of its accumulating on the surface (Madge 1969). The most important decomposers of this litter seem to be fungi, and so effective are they that soil animals are forced to feed on them rather than on the dead litter. Thus, earthworms, in contrast to their role in mid-latitude soils, do little digging of the soil, so the organic upper horizon is usually marked off sharply from the mineral soil beneath. The role of fungi in the nutrition of higher plants is still uncertain. In some authors' views, 'direct nutrient cycling' may take place, whereby mycorrhizal fungi act as both decomposers and direct channels of transport to higher plants.

Others challenge this (Anderson *et al.* 1983) and point to the complexity – largely unknown in detail – of the decomposition process in these forests. In fact, the importance and mechanisms of the detrital pathway of energy transfer in most forests, temperate or tropical, have been little investigated or understood in spite of the attention that has been paid to nutrient transfer (Jordan 1985).

A number of studies reveal the surprisingly low biomass of animals in these forests. Most of the vertebrate fauna is represented by the bird population, but some of the mammals are important in nutrient cycling. Thus, in the Americas, tree sloths (*Cholopus*, *Bradypus*) have been shown to consume 0.63% of the total leaf production in the study area ($53 \, kg \, ha^{-1} \, y^{-1}$), and their droppings, which decay slowly, form an important nutrient reserve (Montgomery & Sunquist 1975). Invertebrate fauna, especially termites and leaf-cutter ants, also exert effects on the ecosystem, especially by their selective behaviour (Lugo *et al.* 1973, Haines 1975).

As with the case of production rates, earlier estimates of plant biomass seem to have been too high and more recent figures have consistently revised these downwards. For example, Fittkau and Klinge (1973) suggested a total plant biomass of around $1100 \, t \, ha^{-1}$, which seems now to be too great. Brown and Lugo (1984) suggest that the plant biomass for closed, broad-leaved forests may average

no more than 176 t ha^{-1}, and around 61 t ha^{-1} for open, broad-leaved tropical forests. These figures are much less even than those obtained for Thailand forests of 360 t ha^{-1}. Brown and Lugo suggest a world
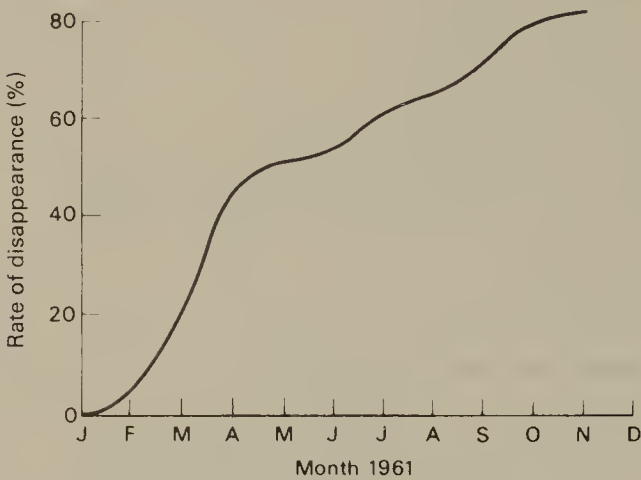
Decomoosition of oak leaf discs in a deciduous wood in Hertfordshire, England
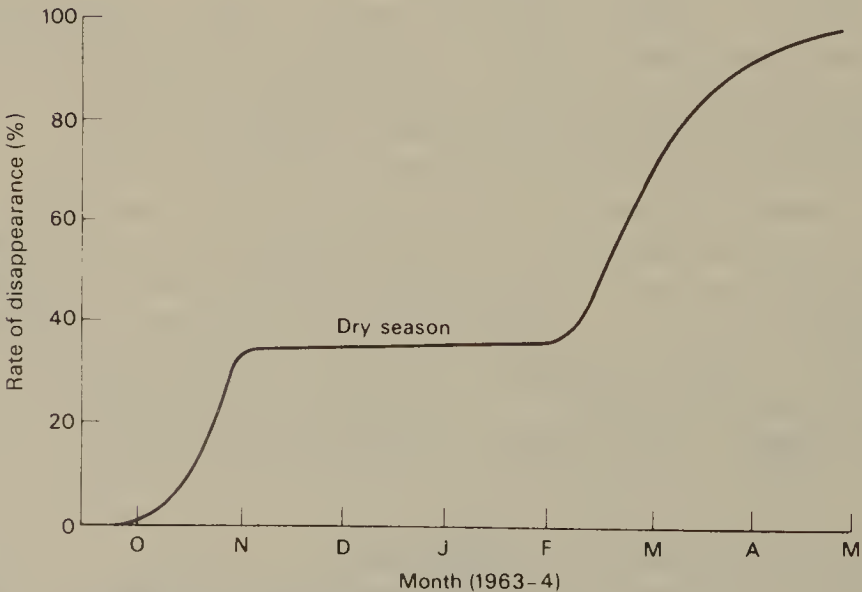
Decomposition of leaf discs in a tropical seasonal forest, Ibadan, Nigeria (mean results of four tree species)

Figure 9.5   Decomposition of leaf discs in tropical and temperate forests. (After Madge (1966).)

total for tropical forests of all types of 205×10^9 t. The discrepancies in figures for even this most basic measurement are indicative of our continuing ignorance of much of the fundamental ecology of these vital formations. One thing is fairly certain, however, and that is that the intense level of biological activity of the rainforest is maintained by a massive cycling of mineral elements, 3–4 times the amounts involved in other mature forests. By far the greatest element in circulation is silicon, with nitrogen, calcium and potassium next in importance. The key role in sustaining the massive biomass of the rainforest appears to be played by the nitrogen cycle. Apart from the massive litter circulation, any losses are made good by abundant nitrogen-fixing micro-organisms in the soil – bacteria, fungi and blue-green algae. These populations are themselves dependent on the ample energy-rich material supplied by the vegetation. In virgin forests, analyses indicate that soil nitrogen deficiency is rare. Many of the frequent legumes do not seem to form root nodule symbiosis with nitrogen-fixing bacteria, although one non-legume that does, *Casuarina pupuana*, has become important in managed crop rotations that are replacing haphazard shifting cultivation in the New Guinea highlands.

In spite of the huge circulation of nutrients, numerous observers have commented on the poverty of the soils from which they are drawn. Along with the comprehension of the massive biogeochemical cycles within these forests has come the realization that much of the useful minerals is stored in the living biomass. For instance, one study (Nye & Greenland 1960) found that the ratio of soil nitrogen to biomass nitrogen was practically 1 : 3 and was 1 : 1 for most of the other important macro-nutrients except phosphorus. On their release from the vegetation by rainwash or litterfall or the death of plants, the minerals are taken up by the mass of fungi that infest the soil and returned to the plants very rapidly indeed. So little escapes from the system of circulation that many of the streams originating in virgin forest have a composition *near that of distilled water*.

The tight nutrient cycling of these forests has, however, been questioned by some authors (Baillie & Ashton 1983). There are suggestions that rock weathering may generate significant nutrient input to these soils based on the evidence of plots in Sarawak forests. It appears that the less labile 'reserve' quantities of elements may be supplied by the rock substratum and that this influenced vegetation composition in their study area (see also Proctor 1983).

The role of fire in these forests is a minor one in relation to nutrient cycling, even though fires do occur occasionally (see Stanford 1985).

9.4   Rainforest soil types

The massive withdrawal of nutrients results in soils poor in the formation of stable organic and mineral compounds. At the same time, under conditions of high rainfall, high temperature and good drainage, the silica fraction of the soil becomes mobilized and leached downwards. These processes result in the most frequent soil type of these forests, the *feralites* (Buringh 1968), red soils that take their character from (a) the high content of iron and aluminium sesquioxides, i.e. oxides with two metal atoms to three of oxygen, and (b) simple clay minerals remaining, especially kaolinite (Fig. 9.6). Other names are also used for these soils – *nitosols* and *ferralsols* (FAO system), *oxisols* (USDA Seventh Approximation) and *latosols*.

Not all the soils below rainforest are feralites, however. Extensive tracts of podsols (*spodosols*) exist in Thailand, Borneo, Malaya, Guyana and the Rio Negro headwaters. These soils, usually developed over highly siliceous parent material (sands, quartzites, etc.), have lost their iron oxides through leaching and are very nutrient-deficient. Yet they can carry a dense vegetation, often forming a distinct formation (heath forest), for example the 'keranga' and 'padang' of South-East Asia. These soils probably receive no nutrients from rock weathering at all and the vegetation relies almost entirely on nutrients carried in by rainfall (Richards 1973). There are also soils described as brown earth types – *cambisols* (FAO), *tropepts* (7th Approx.) – which occur in south-west Nigeria and on recent lavas and seasonally dry mountains in South-East Asia (see Table 6.1).

Most soils in the rainforests are easily damaged by forest removal and careless farming. On a small scale, clearances are soon colonized if sufficient primary forest remains, but on a larger scale, if rapid recolonization is prevented, the upper layers can easily become waterlogged and begin to erode. Once the soil pores are filled with water, a process known as 'plinthization' may set in. As the soil is now exposed to direct insolation, the high evaporation induces strong capillary action, drawing up a stiff mottled clay that gradually fills the pore spaces. If this dries out, an irreversible process sets in and a hard impervious duricrust forms. Once formed, this prevents – or appears to for a considerable time – the regeneration of the climax, which is replaced by xerophytic herbs and shrubs and later simpler secondary forest of the kind found in many parts of South-East Asia.

Traditional farming practices based on small-scale clearances
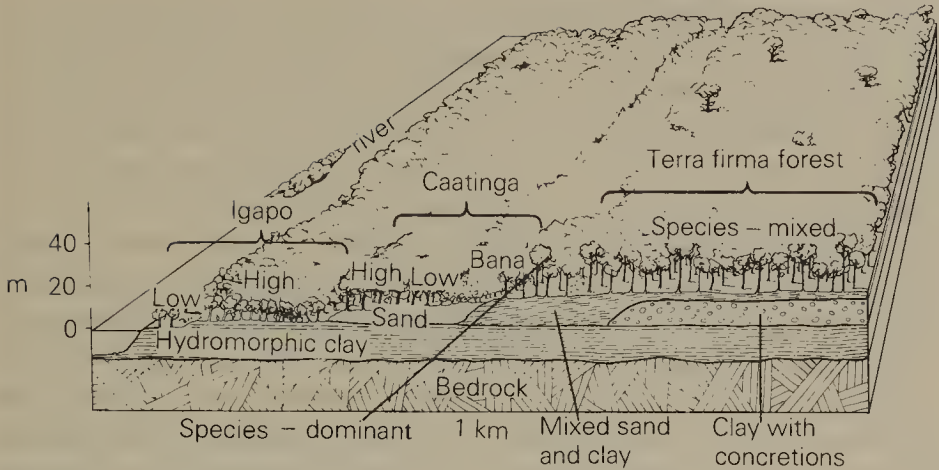
Figure 9.6   Amazonian riverside forest types. (After Stanford *et al*. (1985).)

usually avoided the difficulties presented by the soil characteristics. Rapaport (1976) has shown that such systems can carry surprisingly high population densities given a sophisticated range of crops and the use of pigs. He shows that the wet forests of New Guinea can carry a population density of 124 people per square mile of agricultural land provided all the adults are engaged in farming. At the same time, the forest cover essential for forest regeneration can easily be conserved. However, in the Himalayas, it has been shown that for every unit of energy produced by agriculture, there is a cost of seven units of energy from the forest. Consequently, there are few forests remaining with a reasonable crown cover (Singh & Singh 1987). Western agricultural practices, on the other hand, involving large-scale machinery and wholesale forest clearance, carry great dangers. The successful systems rely mainly on arboriculture for bananas, cacao, oil palm and rubber, which by careful management of the tree cover can be designed to avoid the processes of plinthization and soil erosion. However, the wet tropical forests are at present under increasing attack from timber production, especially in South-East Asia, and in the Amazon for commercial farming in the wake of the Brazilian highway-building programme. In the latter area, although the Brazilian government makes provision in its land sales for the preservation of forest in the 60-mile plots each side of the road, the record of previous attempts to open up this great wilderness for speculative farming lends little confidence that this can be done without serious damage to the ecosystem.

The long evolution of this ecosystem type has produced a battery of mechanisms encouraging stability of the system. Weeds and aliens

are almost never found except where man has intruded. Epidemics of fungal disease, insect larvae and pests seem to be rare in undisturbed forest (Richards 1973). Even the stability of the land surface and the control of erosion rates is part of the forest homeostasis. Little material is released to rivers, so they carry almost no load if they originate within the forests and consequently have almost no down-cutting power. These are the 'clearwater' or 'blackwater' (peat-stained) rivers of the geologist. Any hard bands are crossed as rapids. (These are the habitats of a peculiar plant group, the Podostemaceae, with special adaptations for clinging to rocks.) At fault scarps, waterfalls occur with no potholes at their foot nor any recession. In the Lower Amazon, for example, it has been found that some 80% of the river load is derived from its Andean headwaters, not its huge lowland basin (see Douglas 1969).

As satellite photographs dramatically reveal, these forests are being removed at an ever-increasing rate. One figure suggests that, at the rate current in 1987, it represents approximately the equivalent of the surface area of a country the size of Belgium annually.

9.5   The deforestation process

Figures published by Lanly (1982) for the FAO and by Melillo *et al.* (1985) have shown some discrepancies in estimating current rates of deforestation. The latter group estimates an annual conversion to permanently cleared land of closed tropical broad-leaved forest and fallow cycle vegetation on land once occupied by forest as 4.5×10^6 ha^{-1} y^{-1}. Earlier estimates give higher figures of 6×10^8 ha^{-1} y^{-1}. Whether higher or lower estimates are ultimately accepted, most authors are agreed that (a) the rate is increasing rather than decreasing, and (b) it is vital to establish efficient remote sensing to provide accurate information so as to formulate sensible conservation policies. The latter are needed not only for the conservation of biotic resources but also to help in accurate monitoring of the effects of clearance on the cycling of atmospheric carbon dioxide. Particularly important in conservation strategy is the question of size of reserves in order to allow the possibility of viable reproduction of plants and animals (Kent 1987). The individual plant species may be scattered widely through the forest and, in the case of the rarer species, there is no real idea as to how many individuals may be needed to maintain a viable population. Ng (1983), Hubbell and Foster (1983) and others have highlighted the problem of how large

reserve areas need to be to conserve effectively the flora and fauna of tropical rainforest areas. For example, Ashton (1976) suggested that a minimum of 200 individuals of any tree species were essential to maintain a breeding population in closed rainforest in southern Asia. When it is considered that in species-rich forests individuals of the same, and not necessarily uncommon, species may be separated by some kilometres, the problem of reserve size can be seen as critical. Moreover, to maintain the soil seed bank, on which rapid regeneration depends, needs sufficient area for pioneer species to complete their life-cycles often enough to maintain their seed presence in the soil. Also, these species are extremely important in their role as preservers of the essential nutrients derived from fallen trees in gaps. It has been shown, for example, that for four weeks or so after clearance there is a flush of nitrogen in the soil, which is gone by eight weeks, and the pioneer species show adaptation to this with high nitrogen content in the leaves (Servant *et al.* 1984). Also, if phosphorus is not taken up rapidly by woody vegetation, forest regeneration is very difficult. It is this mineral that is particularly marked in its loss (Salati & Vose 1984).

Not least amongst the considerations of clearance of tropical rainforests is the question of its effects on climate. Considerable, and it must be said often alarmist, speculation has been published on this topic, for example its relationship to atmospheric levels of carbon dioxide. On this it is probable that there is little overall effect given the high respiration rates within these formations. However, the major continental vegetation coverage in South America has an undoubted role within the water balance regionally, and this may also be true in the African land mass, although it may have less of a role to play in South-East Asia. The Amazonian forests in particular have been shown to be in equilibrium with the prevailing water balance in the following way. Water vapour in the troposphere above the central Amazon Basin is supplied approximately 50% from oceanic evaporation and 50% from evapotranspiration. However, *rainfall*, derived as much of it is from the water vapour in the lower atmosphere, has 74.1% of its source in evapotranspiration. Of the rain that falls, 25.9% is lost as runoff, 25.5% is evaporated directly from the vegetation surface, and no less than 48.5% is returned by transpiration (Salati & Vose 1984). These figures show that the effects of wholesale removal of forests in this region would entail drastic changes in regional climatic and erosional conditions (Sioli 1985). Already, upstream removal of forests in the Bolivian Andean selvas has produced a marked changed in flood levels recorded at Iquitos,

where water levels in above-average floods have risen by 1.5 m on average since 1962 (Genry & Lopez-Parodi 1980). Some speculative consequences of forest removal in South-East Asia have been cited as affecting the albedo of the seas near islands where active deforestation is taking place. The increased turbidity due to the addition of river-borne material, it has been suggested, has resulted in alterations of the sea temperatures and has major effects on ocean currents. The phenomena of 'El Niño' has also been linked to this. (For a discussion of the effects of vegetation on climate, see Lockwood (1980, 1983, 1987).)

It should be clear from this section that conversion to permanently cleared land of these complex ecosystems is no easy matter. Actions are taken daily in the steady destruction of this vital biotic and environmental resource, yet this inexorable process is based on so little knowledge that we have no real inkling of the consequences. In fact, our only certain knowledge is that we do not know what we are doing.

9.6   Variations in tropical wet forests

In the equatorial regions, the ascent of lowland rainforest to higher levels is scarcely marked at first as ascending air masses shed copious water. The most notable change in physiognomy is the increased numbers of epiphytes. At cloud level, the distinctive cloud forest develops and can be found between 1000 and 2500 m. Here, the constant humidity produces a profuse growth of epiphytes for which these forests are most noted. The epiphytes are not the angiosperm types of the lower forests but the mosses, lycopods, ferns and especially the filmy ferns (*Hymenophyllaceae*), which form a green coating to the trunks and branches of the trees. The trees themselves are smaller than their lowland counterparts. The forest floor is often covered with *Selaginella* spp. and tree ferns. In Africa, the wettest parts often have dense bamboo thickets, and in South America, under the same conditions, plentiful palms. What sets the altitudinal limit to montane forest is not certain, but it gives way to a shrub zone with, by this stage, signs of podsolization in the soils and in some areas gleysols with peat.

Studies on montane forest in Jamaica (Janner 1985) indicate that these forests may have significant nutrient deficiencies when compared to lowland wet tropical forest. In particular, nitrogen, phosphorus, potassium and calcium deficiencies were noted. In the

Himalayas, it has been shown that the species composing the montane ecosystems are highly adapted to take advantage of monsoon rainfall (Singh & Singh 1987).

In lowland sites along rivers liable to flooding or where soils are permanently waterlogged, variations of formation-type are introduced that are distinct from terra firma forest in both species composition and number. In general, these forests have an impoverished flora (Lieberman *et al.* 1985). Also, in seasonally flooded forests, rates of net primary production (NPP), litterfall and biomass turnover are higher than would be predicted from climatic conditions, while rates of wood production and storage of organic matter in vegetation and the soil profile are below expectation (Frangi & Lugo 1985).

9.7   Seasonal tropical forests

The major formations that display these characteristics occur in South and Central American (Venezuela, Guyana, north-east Colombia, western Costa Rica, along a belt at the southern rim of the Amazon Basin and parallel to the coast in south-east Brazil), in South-East Asia, West and Central Africa, and Queensland, Australia.

The transition from evergreen rainforests to those with a greater number of seasonally deciduous species has been related to increasing length of dry season and decrease in rainfall (Fig. 9.3). However, as shown in Figure 9.7, both the amount of deciduousness displayed and the number of species liable to shed their leaves vary acording to soil type and altitude in any particular climatic regime (Webb 1968). Forests that can be ascribed to this type are much more variable in structure than rainforests, as the increasing moisture stress has provided greater opportunities for the development of adaptive features of life-history and life-form.

Unlike most of the rainforests, formations in this category often exhibit dominance by a few species, as in India and Burma where the sal (*Shorea robusta*), teak (*Tectona grandis*) and *Terminalia* species form major stands in the so-called 'monsoon forests'. The seasonal forests have almost a wintry appearance in the dry season, but some observers have emphasized that it is in this season that many species flower. Those that flower – especially herbs – at the end of the wet season have been noted as responding to the seasonal variation in day length. Although the seasonal forests and rainforests may share few
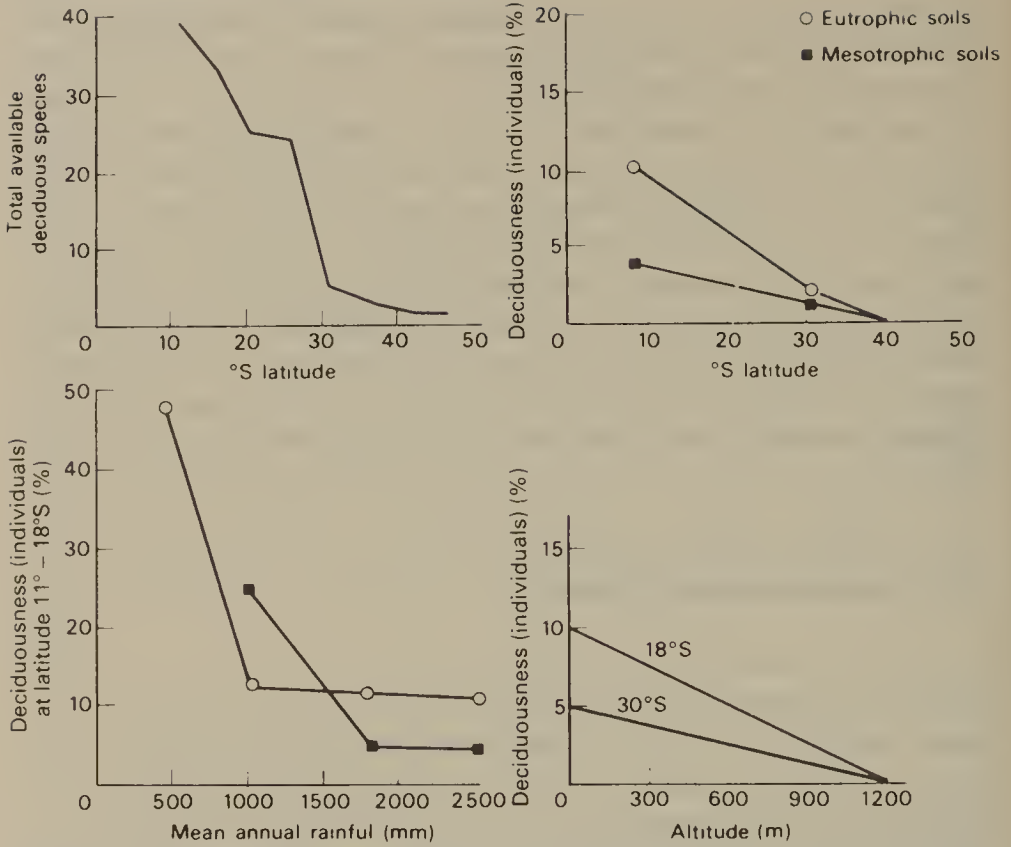
Figure 9.7 Diagrams illustrating the relation of deciduousness to various environmental factors in eastern Australian forests. (After Webb (1968). © Ecological Society of America.)

plant species they may nevertheless be intimately connected in other ways. For example, Janzen (1987), after many years of intensive study of the western seasonal forest of Costa Rica, has shown that moth populations which are highly significant to pollination of many seasonal forest species, undergo extensive regular migrations between seasonal and evergreen forests.

Biomass, production and mineral cycles

Living plant material in these forests appears to average about 205 t ha^{-1}, but there are considerable differences between the wetter and drier ends of the climatic spectrum under which the forests develop. In contrast to the wet tropical forests, the dry season slows the destruction of litter (Fig. 9.5), and greater quantities of dead material can accumulate to form a significant part of the total organic matter. The amount of dead material is also variable according to climate,

there being usually a much more efficient destruction by soil organisms in the wetter types. Where the dry season is longer and the material resistant to attack, as with bamboo thickets in South-East Asia, the quantities of dead organic matter can be considerable. In one study in Thailand, as much as 19–20 t ha^{-1} of dead bamboo was recorded.

The mineral circulation may have more in common with that of the temperate forests than with the hot wet forests, especially as regards the proportions of the various minerals in circulation. However, there are few studies on which to base more than tentative conclusions.

The occurrence of fire in these forests introduces an ecological factor of considerable significance when compared with the hot wet forests. A dry season, even if only a few months long, combined with accumulated undecomposed litter, produces perfect conditions for the incidence of fire. These need not be annual to have marked effects. Occasional fires, possibly at long intervals, might well be sufficient to exclude the species of the hot wet forests. These have been shown by experiment in forest reserves in West Africa and India to be perfectly capable of colonizing the wettest seasonal forest, but their thin bark and unprotected buds make them easy victims of fire.

Soil conditions

The soils of these forests are not the feralites of the hot wet forests, although they may often be red in colour. It seems that where precipitation is below 1500–2000 mm per annum, feralites rarely form (Ackroyd 1967) and the clay–humus content is much more stable with a greater reserve of available bases. Their frequent reddish colour is due to the mobilization of iron, which tends to form concretions. Although they need careful management, the more eutrophic types can be made very productive. In many parts of the world, especially South-East Asia and Africa, many of the forest areas have long been cleared or kept in some form of broken climax for a considerable time. Thus, it is impossible to get a true idea of the climax or of the original nature of the soil. In South America, the forest and soils are much less disturbed and it has been suggested that the frequent dominance by valuable species and the rapid regeneration rates – possibly about 100 years to maturity – make these lands more suited to forestry on a sustained-yield basis than to agriculture. However, whether the world has time to work out proper management techniques for these soils is a moot point. Some of the most rapid increases

in world population are associated with lands formerly or now partially dominated by these forests. South America, West Africa, the Indian subcontinent and South-East Asia all have rapidly expanding populations dependent on the capacity of these soils to supply food and raw materials for industry. Various world agencies and local institutions are engaged in many experiments to improve the agricultural practices, crop types, land management techniques and economic infrastructure in order to maximize the potential of the soil, but it is undoubtedly a race against time. After the great world food conference in Rome in 1974 it would seem that, for the foreseeable future, the surpluses of the soils of temperate lands must underwrite the deficiencies of these soils (see Brundtland 1987).

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10

Tropical formations with conspicuous grasslands: savannas

There are a number of definitions of the word 'savanna', which in origin is an Amerindian term. In Europe, it is usually defined as a tropical grass-dominated formation with a greater or lesser proportion of open woody vegetation and associated trees. In the USA, the word 'savanna' is not confined in its usage to tropical formations. These rather vague definitions have challenged a number of authors to define the vegetation type more precisely. Walter (1984) excludes formations that are not natural in origin. However, others make no such distinction. As research has proceeded within these lands, it has become increasingly clear that their ecology – superficially similar from place to place when judged by appearance – is very complex. Indeed, no better example of the complex, intricate mosaic patterning of communities can be found than those which exist in the savannas.

Savannas exist in *all* tropical climatic regions and are neighbours to practically all the tropical formation-types. They cover some 20% of the world's land surface and are found in both mountain and lowland areas over a variety of soils. With such a diversity of habitats, it is hardly surprising that their origins and ecosystem dynamics should be the subject of active controversy.

10.1   Physiognomic and botanical character

Floristically, the herbaceous layers tend to be strongly dominated at any particular locality by one or two species of various genera (*Andropogon*, *Loudetia*, *Hyparrhenia*, *Pennisetum* and *Stipagrostis*, and in Australia *Themeda*, *Astrebla* and *Triodia*). The height range is

from the several metres of African elephant grass (*Pennisetum purpureum*) through the habitual one metre or so to the low sparse grasses of areas with a long dry season. All the grasses are xeromorphic and many have rhizomes (underground stems) and densely tufted aerial parts.

The shrub and tree strata are diverse and contain numerous species that display similar morphology. Their rooting is strong and may attain great depth, and their crowns are often flattened with small, hard, dry leaves shed during the dry season. Some, such as *Acacia faidherbia albida* of the African Sudan-zone savannas, retain their leaves and many (except in Australia) are thorny. Most have thick bark and bud scales, which preserve them from fire and desiccation. Both trees and shrubs produce enormous numbers of seeds. *Acacia karoo*, for example, may release 20000, 90% of them fertile, most of which are eaten by termites, destroyed by fire or fail to establish themselves after germination.

The subject of competition between grasses and trees is complex and the reader will find various opinions held by different authors. Walter (1984), for example, believes that they are direct competitors, especially for water at the end of the dry season. As grasses can withstand considerably greater drought than trees, they should be more successful on fine soils where their dense rooting can more easily command their soil moisture reserves. On stony soils, on the other hand, trees should be more successful as their deep roots can better exploit reserves at depth. Thus, on stony soils, Walter envisages trees as being the true dominants, with grasses only a tolerated part of the community. He presents the following scheme as indicating the main plant–climate–soil interrelationships in summer rain areas (i.e. most of the savannas):

(a) stony soils dominated by woody plants;
(b) fine soils (250–500 mm mean annual precipitation) dominated by grasses with some woody plants;
(c) fine soils (over 500 mm mean annual precipitation) associated with savanna woodlands;
(d) fine soils (100–250 mm mean annual precipitation) dominated by pure grasslands.

The view that grasses and trees are direct competitors may well be valid. However, there is considerable evidence to show that grasses and trees can coexist to form stable communities under a variety of climates and on many soil types. Moreover, the patterns of grass–tree

associations have been very convincingly related to the mosaic of the soil and geomorphological units inherited from Tertiary times and modified profoundly during the last two million years.

10.2 Environmental relationships

It is now quite clear from both observational and experimental evidence that the savannas are multi-factorial in the ecological relationships that maintain them and, although superficially grassland may offer a generalized description of the vegetation type, the factors that sustain their presence vary widely from place to place. In reviewing these factors, Werger (1983) both redefines the formation-types that are commonly placed under the broad heading of savanna, and identifies five principal factors that condition their existence. The four principal formation-types are given as follows:

(a) grassland – trees less than 1% surface coverage (i.e. more than 30 tree crown diameters apart);

(b) savanna – trees 1–10% coverage (8–2 crown diameters apart) plus, in some areas, thickets or bush clumps 1–10% coverage;

(c) dense savanna – trees or shrubs 10–50% coverage (2–⅓ crown diameters apart);

(d) savanna woodland – dominant tree layer canopy 50–90% coverage (trees less than ⅓ crown diameters apart); shrubs in the undergrowth; grass well developed but not very dense.

Werger (1983) lists the five factors that together determine which of the above types is present at any particular place as: climate, soil, hydrological and geomorphological factors, fire and grazing. In reaching this conclusion, Werger brings together the results of the large number of observations that have been made on the ecology of this vegetation type over many years by many authors, who individually may have emphasized one or the other of these factors as paramount within the areas they have studied. By and large, the question of the anthropogenetic origin of some savannas is not considered.

In India, as in other parts of the tropical world, areas that have climatic regimes appropriate to the development of seasonal forest (heavy, warm-season rains and cool-season drought) have much of the land surface occupied by grasslands. The reasons for this are variable but may be ascribed broadly to two main causes. The first is

the impact of farming systems, either permanent clearance for sedentary agriculture as in India and parts of South-East Asia, or temporary bush fallowing in slash-and-burn economies. The latter are widely practised throughout the tropical world and, although fallowing allows the re-establishment of woody vegetation, increasing population pressure allied to uncertain rainfall, for example in areas such as the Sahel, have reduced both the length of the fallow period and the available moisture necessary to encourage the establishment of woody vegetation.

The second set of factors derives from the geological and geomorphological character of many of the regions with climates suitable to seasonal tropical forests. One example from the Matto Grosso in Brazil has already been outlined in Chapter 8, where the influence of soil texture on the grass–woodland balance was demonstrated. More generally, large areas of Africa, India, Australia and Brazil are dominated geomorphologically by ancient erosion surfaces inherited from Cenozoic times. The soils overlying many of these surfaces on non-volcanic rocks tend to be deficient in nutrients, so that, once forest is removed, its re-establishment is very difficult. Moreover, many of these surfaces are underlain by impermeable barriers, preventing water penetration to depths where it could be stored and tapped by trees. Tinley (1982), for example, found on a 200 km traverse in East Africa that the 7 m trenches he excavated uncovered these impermeable layers inimical to tree growth at most sites. Most of these crusts are of fossil origin and developed during the Pleistocene, when many areas currently within tropical wet–dry climatic regimes were more arid.

We now look at each of Werger's five factors in more detail.

Climate

The generalized relationships developed by Walter (1984) outlined above hold good for much of the savanna lands. In the Indian subcontinent, Walter has suggested the climatic relationships of savanna as reflecting precipitation and length of dry season (Fig. 10.1). Werger (1983) notes that, in West Africa, areas with 150–300 mm mean annual rainfall have only ephemeral grasses, but areas with 300–500 mm are grassy savannas. Only in areas with over 500 mm mean annual rainfall does woody vegetation assume importance. He also points to an aspect of climate usually ignored by many authors, namely the effect of frost, and suggests that the vegetation in southern Brazil, southern Transvaal, the Nyika plateau in Malawi,
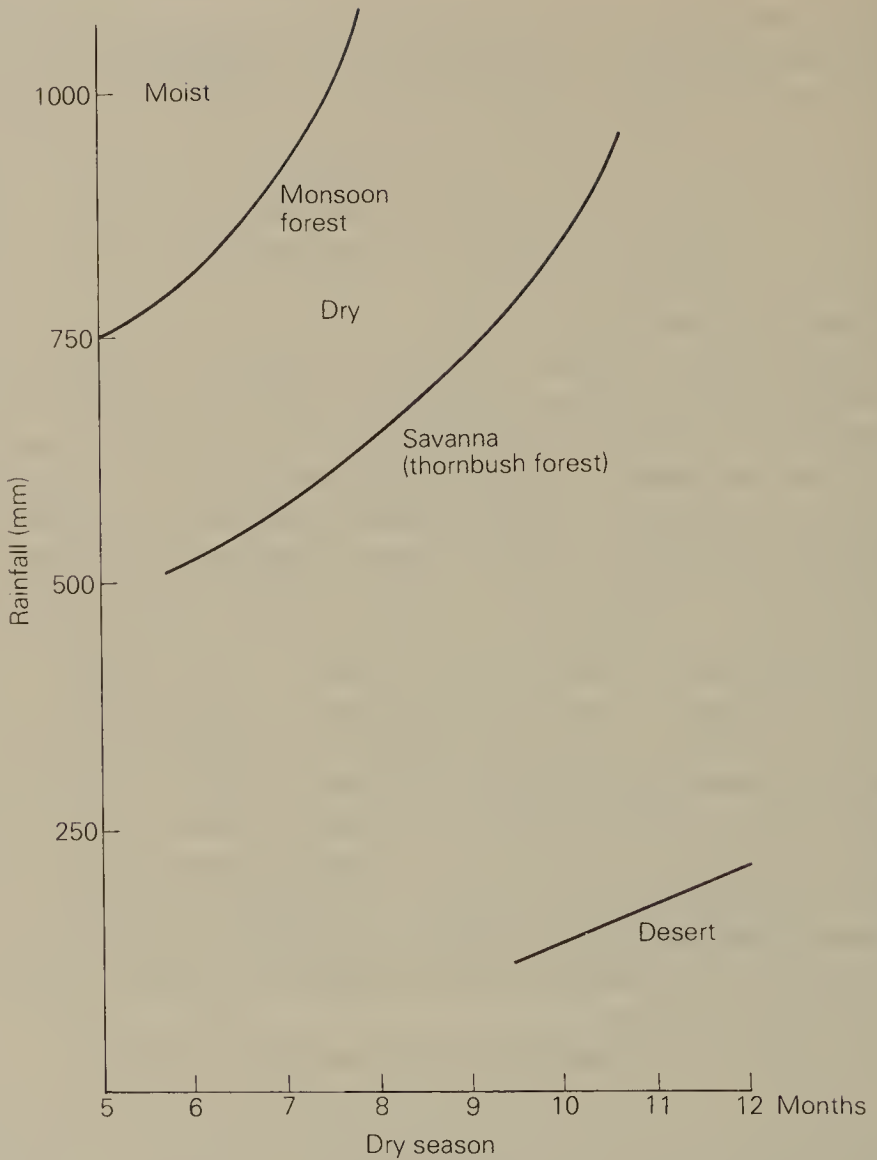
Figure 10.1 Relationships of savanna vegetation type to rainfall and dry season length in the Indian subcontinent. (After Walter (1984).) Note that in this continent much of the land surface with climatic characteristics suitable to savanna vegetation is occupied either by thornbush forest or land cleared for agriculture.

the highlands of Angola and New Guinea mountain ridges may be influenced by this. Also, in southern central Africa the enormous areas of land covered by miombo woodland may be related to frost resistance in the tree types dominating these formations (Walter 1984). Certainly, there are reports of frost damage to trees in these tropical lands, and Werger suggests that, where frost is a regular feature of the habitat, broad-leaved or fine-leaved thorny woodlands

and savannas may be encouraged. Frost also appears to be particularly significant to many species in the savanna after fires.

Soils

Werger relates a number of formations to the nature of soil depth and texture. On deep sandy soils with more than 900mm mean annual rainfall, broad-leaved woodlands are likely with fibrous tuft grasses adapted to leached and drought-stressed soils. Heavy clay soils are associated with woody vegetation, usually with finely divided compound leaves in higher-rainfall areas, and grassland or dwarf shrub communities in lower-rainfall areas. The large areas of termite-mound-derived soils are particularly associated with dense clumps of bush vegetation with grassland rich in nitrogen. This vegetation Werger calls 'bushclump savanna'. Areas of termite-mound soils poorer in nitrogen seem to carry mostly grassland. South American savannas appear to have similar vegetation types associated with areas derived from the nests of leaf-cutter ants. Organic, hydromorphic, peaty soils are usually covered with a dense sward with few trees or large shrubs. If these are strongly clayey, they are often characterized by long, low, parallel ridges and troughs termed gilgai, the ridges and troughs carrying characteristic species combinations.

More extreme soil conditions that determine vegetation patterns are the halomorphic soils and soils rich in metals. The former, where very unfavourable, carry an open vegetation with low, often stoloniferous, grasses with or without a low shrub or tree layer. In more favourable conditions, the vegetation can be a fairly dense covering of dwarf shrubs of species that can develop into trees in non-halomorphic soils. In many tropical grazing lands, saline soils with open or nearly bare sites form relatively small patches in wider woodland or savanna landscapes, while alkaline soils more often cover extensive ranges, for example in East Africa (Unesco 1979). Soils with heavy metals over serpentine rocks strongly determine the vegetation by markedly reducing the tree or shrub layer, and encouraging tolerant grass species. At wetter sites, toxicity is higher than at drier ones, but both are usually rich in endemic species. A particularly notable example is that of the Great Dyke of Zimbabwe, which runs as a ridge for 500 km across the landscape. Even light metals can affect the vegetation. Aluminium, for example, has been linked to the occurrence of more open cerrado vegetation in Brazil (Eiten 1972).

As noted in Chapter 6, the occurrence of concretionary ironstones

(also called laterites in some texts) is widespread in these lands. Although they may have been formed under wetter climatic conditions and represent fossil ferralites, their presence close to the surface induces important vegetational effects especially in the way they shallow the soil.

The influence of the soil factor in determining whether forest or grassy vegetation develops is well exemplified by the campos cerrados vegetation of Brazil, which covers some 2×10^6 km^2 of the country. Here, the nutrient-deficient soils developed on the granitic and siliceous basement rocks support deep-rooted evergreen trees able to tap stored water where no barrier to water penetration exists. These trees, usually between 4 and 9 m high, vary in their surface coverage from 3% to as much as 30%. Grasses and shallow-rooted trees that cover the remaining area are unable to tap this stored water and lose their leaves in the dry season. Under the same climatic regime in the states of Sao Paulo and Minas Gerais particularly, the presence of basaltic rocks with greater nutrient availability allows the growth of formerly extensive semi-evergreen forest. On the other hand, given suitable species, the former soils can carry forest plantations, which have been extensively developed in the two states using *Eucalyptus* species tolerant of nutrient scarcity. *Eucalyptus* species, in fact, have been widely employed in many tropical and subtropical countries to overcome limitations posed by soil and climate. The evolution of this genus over a long period in Australia has produced species and varieties adapted to a wide range of temperate and tropical environments with variable and often uncertain rainfall regimes, as well as difficult soil conditions. This genus, and the equally adaptable Australian *Acacia*, have been aptly described as Australia's gift to the world.

In areas with water tables near the surface which periodically rise very close to the surface itself, the impeded drainage that results often leads to inundation (Vareschi 1980). The effects of inundation are part of the hydrological and geomorphological factors that have been seen to be of particular importance in these savanna environments.

Hydrological and geomorphological effects

The work of Cole (e.g. Cole 1960, 1965, 1987) on the mosaic of community patterns in South America and Australia has pointed to the importance of appreciating the geomorphological history of these lands as a key to the understanding of vegetational patterns, and the

work forms the basis of much of the mapping and description of the Commonwealth Scientific and Industrial Research Organization (CSIRO) in Australia. Cole (1965) identifies four major soil–vegetation units as successors to the widespread plains developed in these lands during the Pliocene and destroyed by the changed erosional circumstances induced during the Quaternary. Figure 10.2 sets these out schematically. Within each of the major associations are a number of minor associations reflecting differences in microclimate, relief, soil texture and mineral status. Thus in (D) on Figure 10.2 the drainage lines from the slopes would contain grasslands called dambo grasslands in Africa.

Cole's analysis of environment–vegetation relationships contrasts strongly with the purely ecological approach of authors like Walter in its explanation of savanna community patterns. Werger points out also that many sharp boundaries between woodland and grassland in these lands are possibly better seen in relation to current hydrological characteristics of the landscape rather than being entirely related to geomorphological history. The latter approach, however, does pro-
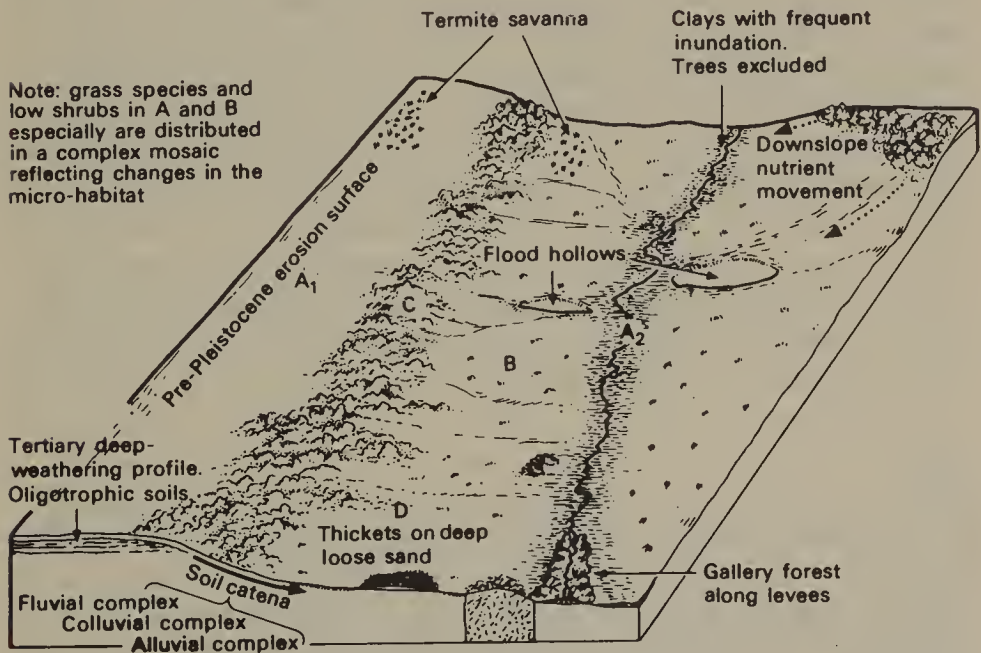
Figure 10.2 Savanna landscape types according to Cole (1965). (A) Pure grassland: A$_1$, grassland on plateau watersheds (low nutrient soils); A$_2$, valley floors with clay soils. (B) Savanna parkland (frequently located on eutrophic or mesotrophic soils). (C) Savanna woodlands (grass stratum present although tree crowns contiguous) generally associated with soils on old erosion surfaces. (D) Low tree and shrub savanna often on most recent skeletal soils.

vide satisfactory accounts for the occurrence of watershed grasslands and floodplain grasslands. Interestingly, one author (Beadle 1981) eschews the use of the term 'savanna' altogether for the continent of Australia. On the other hand, Walker *et al.* (1981) designate all Australian lands with sparse forests, where the herbaceous layer covers over 2% of the ground, as savannas. One intriguing piece of evidence is cast on this controversy by the vegetation of south-west Australia. Here, extensive 'fossil ferralite' soils cap the highest erosion surfaces, and carry a vegetation dominated by jarra (*Eucalyptus marginata*) and karri (*Eucalyptus calophylla*), which would, on the criterion of Walker and his coworkers, be classed as savanna woodland. This vegetation has been described as a 'relict ecosystem' that originated under a more tropical climate with a summer rainfall regime and survives under a warm temperate winter rainfall regime. Its persistence has been ascribed to the extremely base-deficient soils, which have excluded plants better adapted to the climate. If it is correct that this is a relict ecosystem, it is yet another and spectacular example of 'vegetational inertia'.

Where flooding is frequent, the composition and structure of the grasslands vary with the length of the flooding period, and the occurrence of shrubs or trees can also be related to this factor. In non-flooded areas, hydrologically determined vegetation patterns can nevertheless occur, for example in areas of sand or loamy sand with permanently high water tables. In both South America and Africa, woodland vegetation gives way to a more open savanna of grasses and a few species of broad-leaved trees coincident with such sites. In northern South America, *Curatella americana* and *Byrsonia crasafolia*, and in Africa, *Parinari curatellifolia* and *Terminalia sericea*, are characteristic of damp sandy sites. If still higher water tables obtain, trees are usually excluded altogether.

Fire

Some of the savannas of northern South America appear to be Pleistocene relics maintained by fire, and arguments have been advanced for savannas in Borneo, Nicaragua, West Africa and Indochina as having their origin in anthropogenetic burning. By and large, where the annual net primary production is below $1\,t\,ha^{-1}\,y^{-1}$, fire seems unable to sustain itself, i.e. where mean annual rainfall is below 300 mm. Above this level, fire impact on vegetation depends on a number of distinct factors: firing season (damaging fires are more likely at the end of the dry season); the time of day at which

fires occur (higher humidity periods produce cooler fires); and wind strength and direction. Of these factors the most important is the time of year. Its importance has already been emphasized in Chapter 7 in relation to the experiments carried out near Ndola in Zambia and in the Ivory Coast. In one study in Central America (Belize), results show that savanna ecosystems appear to be well able to withstand the effects of fire in their retention of nutrients. Even oligotrophic soil–vegetation systems held their nutrients well. In the absence of fire, nutrient losses from savanna soils are very low indeed (Kellman & Sanmagudos 1985).

Grazing

Many authors have dealt with grazing and its obvious effects through bush encroachment when its intensity becomes too great for the sward to support. The major cause of this phenomenon seems to be the shift in reliable water as the grass cover is destroyed and the surface opened up. Only deep-rooted, woody plants can exploit this deeper water (Walter 1984). One of the most striking examples comes from Botswana, where, in the period 1940–45, double stocking of grazing lands began and its effects were observed by aerial photography. Aerial surveys were undertaken in 1950, 1963 and 1975, and the stocking rate of one beast per 5.6 ha was maintained. The resulting bush encroachment by *Acacia* spp. rose gradually to a level of 10000–20000 kg ha^{-1} fresh weight of above-ground vegetation.

In more natural conditions, on the other hand, grazing can now be seen from experimental work to have a positive effect on the maintenance of the sward. This has been studied extensively in the Serengeti by McNaughton (1979, 1984, 1985), who showed that, in areas where large herbivores concentrate during the wet season, the net above-ground primary productivity of the field layer is strongly regulated by grazing intensity. Under moderate grazing pressure and sufficient moisture, the productivity in grazed plots was as much as twice that in ungrazed areas. McNaughton concludes that many of the characteristic structures and properties of natural grazing land ecosystems are the result of a long period of coevolution of plants and herbivores. The reasons for the enhanced productivity are varied and lend weight to this argument. McNaughton lists nine interactions, ranging from increased photosynthetic rates in residual tissues, to the direct effect of growth-promoting substances in the saliva of the animals.

In spite of the varied material that has been published in recent years on tropical grasslands with trees, there are still large parts of the formation-type in which research is lacking. The extensive land of the Gran Chaco of South America, for example, with its many peculiarities of plant and animal life, has very little record in the literature (Walter 1984).

The reader may conclude that the environmental relationships of this important vegetation type are so complex that there is no single model that can encompass its multivarious origins. In particular, a climatic hypothesis must be seen as only a first stage in formulating causative explanations for the occurrence of any tropical grassland.

10.3   Biomass, productivity and mineral cycling

Because of the varied nature of the savanna lands it is impossible to give precise figures to be expected in the living biomass. In wooded vegetation it can be well into the range of closed forest – as much as 150 t ha^{-1} – but sparse grassland without trees may carry as little as 2 t ha^{-1}. In grassland there is a very direct relationship between productivity and rainfall. Mean figures for grass formations in Namibia indicate a rate of 1 t ha^{-1} y^{-1} per 100 mm mean annual rainfall (Walter 1984). However, in woody vegetation this relationship is far from clear, as many of the woody formations are associated with nutrient-poor soils that limit production.

Two important studies have produced precise figures for biomass and production in African savannas. These are from the Lamto savanna in the Guinea forests of the Ivory Coast (Menaut & Cesar 1982) and the Nylsvley savanna in the Transvaal (Huntley & Morris 1978). The former is atypical of much of the savanna lands as it is burned annually and also has a dry period of only one month. Without the annual burning, it would most probably be quickly occupied by plants of the surrounding seasonal forest and rainforest. The low bush and dense tree savanna within the Lamto savanna has a range of 120–500 woody plants per hectare, and a total plant biomass of 11–80.8 t ha^{-1}, approximately twice as much above ground as below. Net production of woody vegetation, leaves and wood ranges from a low of 0.05 t ha^{-1} y^{-1} to a high of 5.53 t ha^{-1} y^{-1}. The net above-ground production of the grass layer, on the other hand, shows little variation from the low bush to the dense wooded savanna, ranging from 14.9 t ha^{-1} y^{-1} to 14.5 t ha^{-1} y^{-1}. Underground net production does show some variation, however, ranging from 19 t

ha^{-1} y^{-1} in the low bush savanna to 12.2t ha^{-1} y^{-1} in the dense wooded savanna.

For the Lamto savanna, Lamotte (1982) obtained figures of energy flow via decomposition as follows: (i) approximately one-third of annual net primary production was mineralized as a result of fires; (ii) probably less than 1% of net primary production is consumed by herbivores, but the decomposition by detritus feeders, especially earthworms, is significant; and (iii) 80% of primary production is decomposed by micro-organisms. Thus, in this instance, the trophic pyramid shown in Figure 3.2 is not appropriate (see also Bouliére 1983).

The Nylsvley studies reveal considerable short-distance fluctuations in plant biomass (phytomass) of the grass layer, with considerable variations from year to year related to variations in rainfall (mean annual precipitation is 610mm). The above-ground plant biomass of the woody producers (*Burkea africana* is the most frequent dominant) is 16.3t ha^{-1}. The phytomass of the grass layer varied not only annually but also widely in relation to position, below trees or in open sites. Measurement over three years revealed maximum values of 235g m^{-2} between the trees (minimum 141g m^{-2}), and 62g m^{-2} beneath them (minimum 16g m^{-2}). Underground biomass of the vegetation is 15.5t ha^{-1}, with half of this biomass between the trees attributable to the roots of grasses. Average annual litter production was calculated as 170g m^{-2} y^{-1}.

Total insect biomass varies between different savanna types depending on the woody species and whether the grass layer is tree-covered or not. The dry mass of insects in *Burkea* savanna is given as 1.00kg ha^{-1}, and 2.50kg ha^{-1} for *Acacia* savanna. In general, the dry mass of insects is higher in the grass layers.

Knoop and Walker (1985) also demonstrate that areal differentiation of areas dominated by *Burkea africana* and *Acacia* spp. is related to soil conditions. The former tends to occur on sandy material with poor natural fertility and a generally low herb biomass, whereas the latter is associated with more fertile siltier soils with a higher herb biomass. They also demonstrated the effectiveness of the herbaceous layer in competition for water resources on open sites. In sandier sites, the greater water percolation gave woody plants the advantage.

The vegetation supports an impressive range of animals, now protected within the National Park of which the Nylsvley savanna is a part. The most important consumers of the living plant material are the rodents, but no figures were obtained for the living zoomass of any of the animal groups apart from cattle, which are allowed to

graze from January to April. At a previous stocking rate of 150 kg
ha^{-1}, bush encroachment was evident and this rate was halved from
1976. Unlike the previous example in West Africa, in the Nylsvley
savanna the most important decomposers are the termites, of which
there are 15 species, four of which consume humus and the rest dead
wood and grass litter. There is some evidence that termites and
earthworms, while not completely mutually exclusive, tend to pre-
dominate in their roles as decomposers at the expense of each other.
Thus, in the Lamto savanna, earthworms play a major role and
termites a minor one, the reverse of the position in the Nylsvley

Woodland dominated
by various species

Swamp complex

Short grassland
(dry, saline soils)

Medium height grassland
(mesotrophic and eutrophic-
mesotrophic soils)

Tall grassland (eutrophic
soils)

N

1–3   indicates feeding pattern
of Thompson's gazelle

1 January to May

2 May to October (dry season)

3 October to January
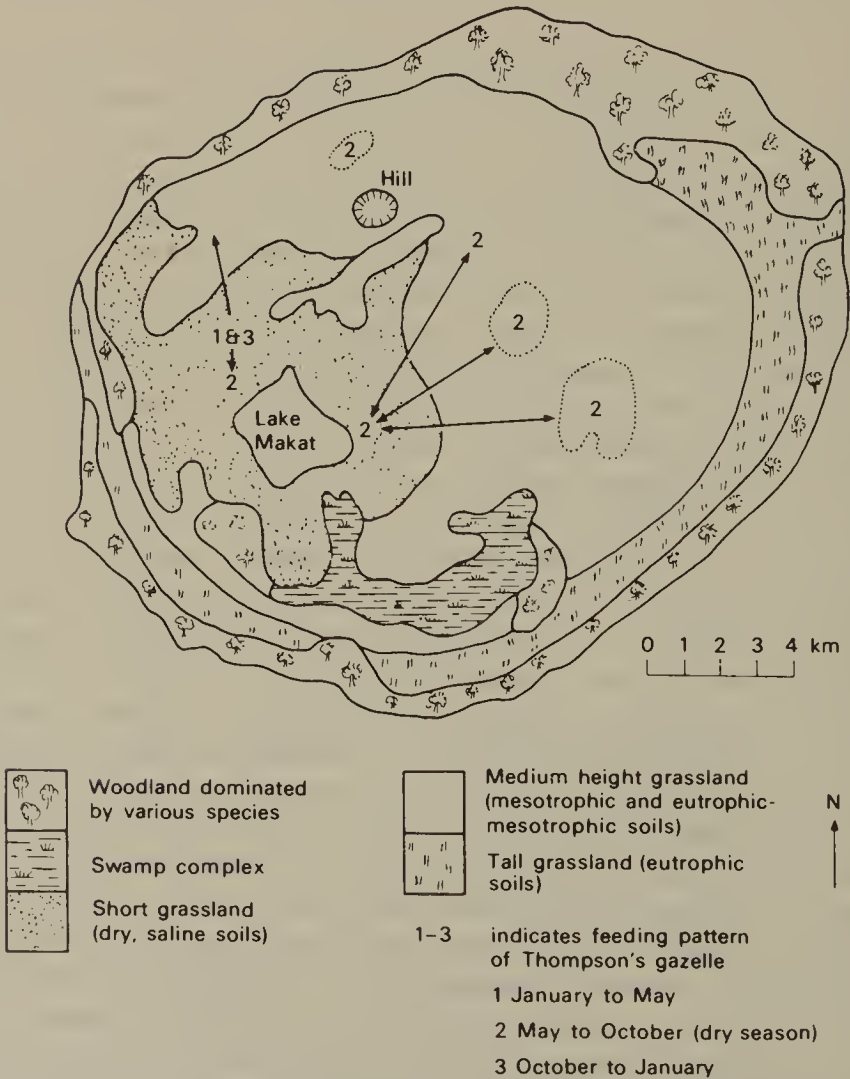
Figure 10.3 Generalized vegetation pattern of Ngorongoro crater, Tanzania. Dotted
areas indicate depressions with *Pennisetum–Andropogon–Cynodon* grassland particu-
larly favoured by Thompson's gazelle. (After Anderson and Herlocker (1973).)

savanna. However, Collins (1981) found in the southern Guinea savannas of Nigeria that termites consumed 60% of annual wood litter, 60% of the grass litter and 3% of the leaf litter, i.e. 35% of the total litter.

Although there are few published studies of mineral cycling in savannas, there are indications that these ecosystems have a marked ability to retain nutrients effectively, for example after fires (Kellman *et al.* 1985). However, Robertson and Rosswall (1986) demonstrate in West Africa that, in relation to nitrogen, although both forest and savanna lose very little under natural cycles, increasing disturbance of the vegetation cover as population pressure rises has become a major determinant of the rates of nitrogen cycling.

There is general agreement that the nutrient circulated in greatest quantity in the tropical grasslands is silicon in both grasses and woody plants. So high is its concentration in some of the grasses that clots of amorphous silica (phytolitharia) may be formed in the leaves. The silica content of the leaves may act both as a defence against herbivory and as a gowth promoter substance (McNaughton *et al.* 1984). The amounts of nitrogen returned to the soil annually are also high and are in fact not far below those quoted for tropical rainforest.

The biomass of soil animals and vertebrates can be very large. In East African thornbush savannas, 250 kg ha^{-1} of soil animals have been recorded, while figures for vertebrate herbivores in East and Central African savannas range between 100 and 300 kg ha^{-1}. Careful studies in the Ngorongoro crater show how so many species in such bulk can be supported (Fig. 10.3). The different game animals each have a particular ecological niche in the way they use the vegetation, and such is the mosaic of plant associations that the animals are presented with palatable food in all seasons (Anderson & Herlocker 1973).

10.4 Soils and agriculture

The substitution of agricultural for natural ecosystems in the savannas is a distinctly hazardous operation in view of the variable nature of the soils, their frequent poverty, their highly variable rainfall from year to year and the many pests and diseases that they harbour. The valley grasslands and parklands can be made reasonably productive, especially with irrigation, but watershed sites and low shrub and savanna woodlands are nutrient-poor and do not take kindly to the plough. Extensive mechanized farming carries with it many risks, for

example soil erosion, soil compaction, rapid exhaustion of nutrients, reinvasion by suckers and the encouragement of pests and aliens where the ecological balance has been disturbed. The peasant subsistence farming of Africa and South America usually avoids these difficulties by the use of shifting cultivation or 'bush fallowing'.

The most important commercial agricultural activity in all three southern continents, however, is cattle raising. As with plough farming, the variable potential of the soil–vegetation mosaic is the most important determinant of forage yield. The mosaic is, nevertheless, open to improvement and management, as the experiments at the Kongwa Ranch in Tanzania have shown. The establishment of exotic pasture grasses on suitable sites allows a carrying capacity as high as one beast per two acres, a far cry from the one beast per several square miles of the Australian outback.

By far the greatest limitation on increasing cattle yield is disease, especially rinderpest, sleeping sickness and foot-and-mouth disease. Although, in Africa, local veterinary methods can be very effective, as with the practices of the Bamangwato peoples of Botswana, the problems of cattle production can only be solved by widespread and effective preventative veterinary medicine allied to land management research.

As yet the inexorable rise in human numbers in these lands is less immediately pressing than in other parts of the world. Nevertheless, within the next few decades, most of them will need to be brought into a managed system, especially in Africa. Given adequate knowledge and the political will to apply it, there should be no reason why these lands could not support greater numbers and still continue to provide for the indigenous flora and fauna that, in Africa above all, constitute one of man's most spectacular heritages (see Lal 1987).

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11

The temperate deciduous forests

The deciduous forests of the Northern Hemisphere have been profoundly changed by long-established and repeated clearance for settlement and agriculture, even in relatively recently settled North America, so that only remnants remain from which to piece together their original character. Some fragments, such as the much-studied cove hardwood forests of Tennessee, are richer in species than others, so that conclusions about their ecology may not be strictly comparable from area to area. The climatic conditions under which they flourish can also vary considerably, so that marked differences in growth rates can be recorded between one area and another. However, in spite of their varied habitats and species composition, their structure is remarkably similar, as can be seen in Fig. 11.1.

One puzzling aspect about these forests is the fact that they occur only in the Northern Hemisphere. Areas in the southern continents with similar climates are largely dominated by evergreens. It seems possible that this striking difference of biogeography may have its origins in an accident of evolution in the remote past. In the Cretaceous period for some reason – possibly as a response to drought – the angiosperm trees may have developed the deciduous habit during their spread into the Northern Hemisphere, but not in the southern lands.

11.1   Biomass, production and mineral cycles

Quite a number of studies have now been made of the ecosystem structure and dynamics in these forests, and sample figures are set out in Table 11.1. In general, complex communities appear to be able to reach higher biomass figures than simple communities. Thus some of the figures obtained in North America indicate a steady biomass increase until the community is 200 years old, when it appears to level

Figure 11.1 Mid-latitude deciduous summer forest profiles. (A) Woodland near Roanoke, VA (leached brown earths over sand and gravels): Qa, white oak (*Quercus alba*); Qs, post oak (*Q. stellata*); Hi, hickory (*Carya glabra*); Rm, red maple (*Acer rubrum*); Rb, redbud (*Cercis canadensis*); D, dogwood (*Cornus florida*); J, juniper sp.; A, arrow wood; Pi, pine sp. (B) Woodland in Trent Park, Herts, England (leached brown earths over glacial gravels): Qp, sessile oak (*Quercus petraea*); Be, beech (*Fagus sylvatica*); H, hornbeam (*Carpinus betulus*); Sy, sycamore (*Acer pseudoplanatus*); Bi, birch (*Betula pendula*); Qr, pedunculate oak (*Q. robur*); Ha, hawthorn (*Crataegus oxyacanthoides*); Ho, holly (*Ilex aquifolium*); M, melick grass; B, blackberry. Both transects 10 m wide. Example (B) was part of Enfield Chase until the 18th century and the older trees bear signs of pollarding, e.g. the beech shown.

off around 400t ha^{-1} (Whittaker & Woodwell 1968). On the whole, figures quoted for Western and Central European forests of comparable age seem to be lower than this. However, the IBP project of Leningrad University carried out on primaeval mixed oak forest in the middle Dnieper region obtained comparable figures to those of North America of around 431.6t ha^{-1}, divided into 306.7t ha^{-1} for the above-ground phytomass and 124.9t ha^{-1} for below-ground material. Primary production is given as 8.9t ha^{-1} y^{-1} for the trees and 9.6t ha^{-1} y^{-1} for the total plant material, representing around 1% of the incoming radiation (Goryschina 1974).

The distinction that is often made between sun and shade leaves in anatomy, the former being more xeromorphic, appears to make little difference to their capacity for production, as the shade leaves remain active longer in autumn (Schulze 1970).

Table 11.1 Biomass distribution and production in temperate deciduous forests.

	Oak–pine forest, New York	Cove forest, Tennessee	Birch forest, UK	Beech forest, Germany
age (y)	40–45	150–400	42	120
biomass	97	585	47.2	185
(t ha^{-1})	(trees)	(trees)	(trees)	(trees and undergrowth)
leaves (%)	4.2	0.6	1.27	1.4
trunks and branches (%)	61.4	85.9	71	73
roots (%)	34.2	13.5	27	25
net primary production (t ha^{-2} y^{-1})	10.6 (trees)	18.00 (trees)	1.8 (trees)	6.5 (trees)
	1.3 (undergrowth)	0.9 (undergrowth)		

The contrast between the net primary production of these forests and that of the wet tropical forests should be noted. As we saw, the latter at maturity seem to have very little, most of the gross production being consumed by respiration. Thus the rest of the food chain dependent on the net primary production has a small biomass total. However, in these mid-latitude forests, even very old communities produce an abundant surplus, much of which is passed annually to the soil to the benefit of soil flora and fauna. Some of the variations in biomass and production in these forests can certainly be ascribed to climatic factors. Cloudy, oceanic types with lower summer temperatures inhibit production rates when compared with continental climates. To an observer accustomed to the British Isles, the rapidity of growth that can be achieved by woody plants of the Eastern USA in the subtropical air masses that dominate the summer weather is astonishing.

The amount of minerals stored in the biomass varies according to age and species. At maturity in American forests it can be as much as 7500 kg ha^{-1}, although most other recorded values are less than this: for example, Central European beech forest at 4196 kg ha^{-1}, lime forest in southern European Russia at 2721–3771 kg ha^{-1} and British birch forest at 678 kg ha^{-1}. In percentage terms, the greatest concentrations of nitrogen and the other major mineral nutrients occur in the leaves. Lime leaves, for example, can yield a percentage dry weight of minerals of 7.23% and in the American elm the figure is usually over 9%.

Although most of these abundant minerals are retained by the plant, the minerals remaining in shed leaves are important in

supplying soil animal life with a rich nutrient supply, especially of nitrogen. The annual uptake and return of minerals appears to lie between 200 and 500 kg ha^{-1}, i.e. about half the values for tropical seasonal forests and only a quarter of those in tropical rainforests. Unlike the situation in tropical rainforests, however, many of the minerals are in only loose circulation. Studies on the Hubbard Brook in New Hampshire show a high loss of calcium especially, output in the streams being four times its input from the atmosphere. (On the other hand, nitrogen is tightly held, atmospheric input being twice output.) In tropical conditions this would quickly spell disaster, but in temperate lands rates of rock weathering and lowering of the land surface by erosion ensure that nutrient supply is continually replenished from below, the materials being lifted by tree tap roots, soil creep and, above all, by soil animals.

11.2   Soil types

The rich soil fauna of the *brown forest* (or *brown earth*) soil type characteristic of these formations is also responsible for the constant movement downwards of humus in the soil. The constant vertical mixing ensures – on nutrient-rich material, at any rate – that these soils lack marked horizons (Fig. 11.2). The rich litter supplied to the soil is rapidly mineralized, mostly by animals, in two stages. First, the primary decomposers (millipedes, woodlice, beetles and earthworms) attack the litter and their faeces are important in producing a good crumb structure as well as providing the food for the secondary decomposers (mites, springtails and potworms), which complete the process. Wet material is also broken down by bacteria, fungi and protozoa, and the general attack by the soil flora and fauna is so effective that almost complete mineralization of mild humus is achieved annually, so there is little accumulation on the surface (Fig. 4.3). Only in very wet conditions or with acid humus does litter decompose so slowly, by wetting and bacterial and protozoan feeding, as to produce a peaty surface layer. Profiles in this case are usually marked and the soils may be described as leached brown earths or, with more intense leaching, podsolized brown earths.

Not all soils below these forests are brown earths, however. In the warmer climates of the southeastern USA large parts of the mixed pine and hardwood forests are associated with red and yellow podsolic profiles. In these soils the prevailing higher temperatures encourage mobilization of some of the clay fraction of the silicate
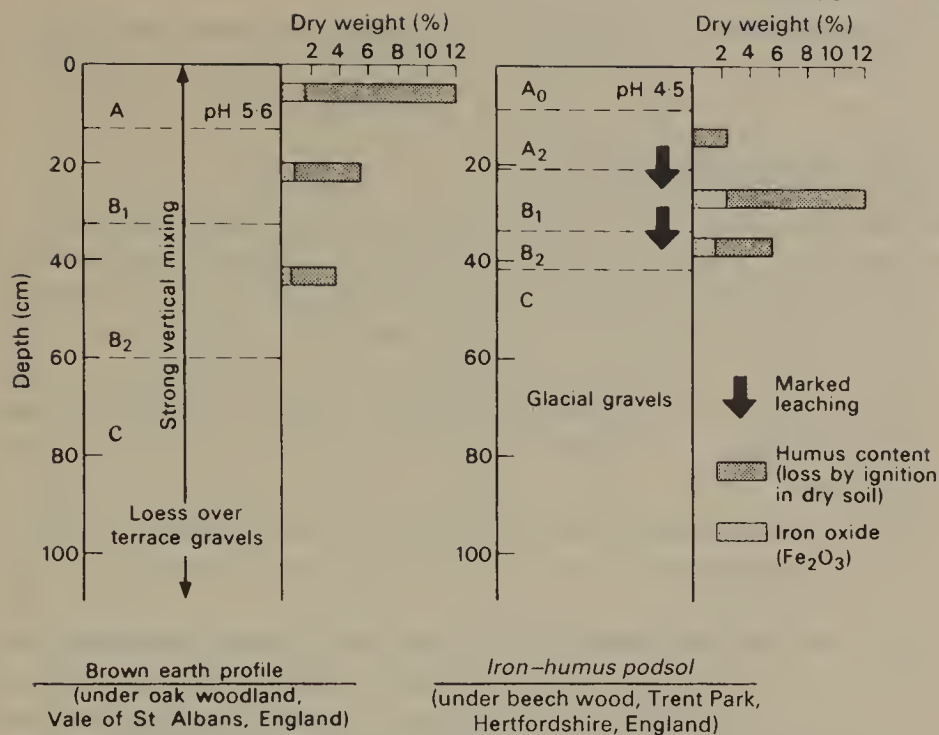
Figure 11.2 Mid-latitude soil profiles. Note in the brown earth profile the horizons are marked by vague transitions rather than the sharp demarcations observable in the podsol. Also, although the podsol is here found under beech woodland, the profile type is observable in almost the same form under nearby coniferous trees. Brown earth profile: A, dark brown; B_1 and B_2, lighter brown; A to C, deeply penetrated by earthworm burrows. Podzol profile: A_0, raw humus; A_2, greyish leached horizon; B_1, dark humus and iron staining; B_2, lighter iron staining (local iron pan nearby); C, no animals present and few roots.

materials, and this is leached downwards. The less stable mineral structure in these types makes them more liable than the brown earths to erosion following deforestation.

On a local scale, the drainage characteristics of soil parent material and its ability to release nutrients have some influence on the geographical distribution of species. In Britain, for example, freely drained gravels may be associated with the sessile oak (*Quercus petraea*), beech (*Fagus sylvatica*), sweet chestnut (*Castanea sativa*) and hornbeam (*Carpinus betulus*), while loams favour the pedunculate oak (*Quercus robur*), the elm (*Ulmus* spp.) and the lime (*Tilia* spp.). On limestones on northern Britain, the ash (*Fraxinus excelsior*) is often dominant, and the wettest soils in all areas usually carry alder and willows. However, there are no hard-and-fast rules governing any of these distributions. Most of the European species are survivors

of very hard times during the Quaternary glacial ages and, as might be expected, are very adaptable.

11.3 Community patterns

The vastly greater number of species in the American and East Asian formations than in the European ensure that community associations are much more complex in these forests. Within the American formations, three major climax types have been recognized:

(a) in the north, beech (*Fagus grandifolia*) and maple (*Acer saccharum*) dominate, with admixtures of conifers like hemlock;

(b) to the south-east, forests dominated by oak (*Quercus montana*, *Q.alba*, etc.) and chestnut (*Castanea dentata*) are frequent; and

(c) to the south-west and west around the southern Appalachians and extending towards the prairies, oaks (*Quercus borealis*, *Q.velutina*, *Q.alba*, *Q.macrocarpa* and others) and hickories (*Carya* spp.) are the most conspicuous elements in the forests.

There is some evidence that this zonation may be the result of the response of plants to both the northwards temperature gradient and the east–west moisture gradient. Within the forests, most associations can be broadly correlated with particular moisture and evapotranspiration values (Fig. 8.1). Evidence suggests that the northern forests were established following the earlier conifer forests around 11000 to 10300 BP, and between 8000 and 4000 BP the area dominated by these formations was stabilized (Shane 1987).

The Asian formations are composed of the same genera (apart from hickory), particularly important species being the native ash (*Fraxinus mandshurica*), birch (*Betula armanii*) and beech (*Fagus crenata*).

In Europe, the common forest species of the north-west are replaced towards the Mediterranean by other deciduous oaks such as the pubescent oak (*Quercus pubescens*) accompanied by evergreen oaks. Towards the east, the beech is absent beyond the Vistula, and from the Ukraine to the Urals the rich loess soils are dominated by the oak (*Quercus robur*) and the sandy soils by Scots pine (*Pinus sylvestris*). At the northern limit of the forests, the dominant tree in southern Scandinavia is the beech.

It is clear from the varying behaviour of trees in these forests, as Lechowicz (1984) has pointed out, that the Quaternary glaciations have had a profound effect on the species that compose them. There now exists, as a result, a general evolutionary disequilibrium between the climatic conditions in which they currently grow and their **phenological** characteristics, i.e. their flowering, fruiting, leafing and so on. The repeated disassemblage of these forests during the Quaternary means that, for example, their patterns of coming into leaf and their internal morphology are only loosely attuned to the climatic conditions. As Lechowicz expresses it, they have been 'decoupled' from the prevailing environment. In the case of leafing, particularly, it is striking that trees in these vegetation types come into leaf at different times: *Populus*, *Betula*, *Salix*, *Alnus*, *Acer*, *Carpinus*, *Prunus* and *Aesculus* are early leafing and all have narrow-diameter wood vessels. Later leafing trees (*Fraxinus*, *Quercus*, *Rhus*, *Ulmus*, *Sassafras*, *Morus*, *Carya* and *Juglans*) have larger-diameter wood vessels produced in their early spring wood and have a ring-porous wood anatomy due to cavitation in winter, which renders capillary columns useless. These trees need therefore to activate cambial tissues preceding leafing. Some of the trees with narrow vessels (*Nyassa*, *Platanus*, *Liquidambar*, *Tilia* and *Fagus*) leaf late, and Lechowicz suggests that this may result from their evolution in paleotropical and semitropical environments, whereas the narrow-vesselled, early leafing types originated in the temperate Arcto-Tertiary floras and have indeterminate shoot growth to minimize losses to late frosts.

11.4   Man and the deciduous forests

Since the introduction of agriculture to these forests by Neolithic farmers (about 6800 BP in Britain (Smith 1974)), the soils and forest resources of this formation-type have been profoundly transformed by the activities of man, but nowhere has the forest disappeared completely. In Europe and the Far East, for many centuries, the forests were incorporated into human farming and land management practices adapted to the sustained conservative use of the forest resource. The economic system was controlled by an armoury of checks and legal rules, which attempted to combine the good of the commonality of people and forest with the needs of the individual for fuel, building timber and pasturage. Systems such as these still operate in parts of Europe and possibly China, but in lowland

England and Denmark, for example, many of them were swept away at the time of land enclosure and dispersal of the farms from nucleated villages. Tenuous fragments of these systems survive, as in the New Forest in England, but even here the system has been disrupted in response to commercial pressures (Tubbs 1970). In North America, the settlement of the eastern forests never produced the extensive clearances of Europe and China, and since the 1940s there has been, in any case, a reversal of the process. The increasing efficiency of mid-western farming has resulted in the abandonment of much of the eastern farmland to tax-loss investment or urban development (Hart 1968), with the rapid reinvasion of trees of the early seral stages (Fig. 11.3). Probably there has never been so much land covered by the deciduous forests in North America since the beginning of the century.

The soils of this formation are superb providers, responding to good husbandry with generous crop yields. These yields are not simply the product of ingenious technology or the addition of chemical fertilizers. Their natural drainage characteristics, well aerated structure and abundant microbial and animal life give the soils tremendous strength even when abused by heavy machinery and excessive chemical treatment. No better example could be found than the famous Broadbalk field at the Rothamsted Experimental Station (at Harpenden, England), which has produced cereal crops for over 100 years without the addition of fertilizer of any kind. Its nitrogen supply is maintained by the blue-green algae coating the soil crumbs, and other minerals are released from its great reserve of bases. In all that time it has shown no signs of eroding and might appear to be able to go on supplying food almost indefinitely. Soils of this kind formed the base for the growth of prosperous states in northern and western Europe in late mediaeval times and European history has revolved around the centres of wealth and power that these soils fostered down to the present day. The Paris Basin, Aquitaine, Burgundy, Flanders, eastern Jutland, the Rhineland, Saxony, Westphalia, the English lowlands, Bavaria, Bohemia and the Austrian lowlands are still regions with political and cultural meaning, especially as the growth (almost literally) of wealth based on these soils founded most of the great European cities, which focus the life of modern man. The less well endowed soils, especially the podsolized brown earths on nutrient-poor substrates, are more open to abuse and at times in the past have even been so impoverished by farming as to be abandoned. In Britain, for example, the soils of the North Yorkshire Moors overlying coarse sandstones were overgrazed by Bronze Age farming
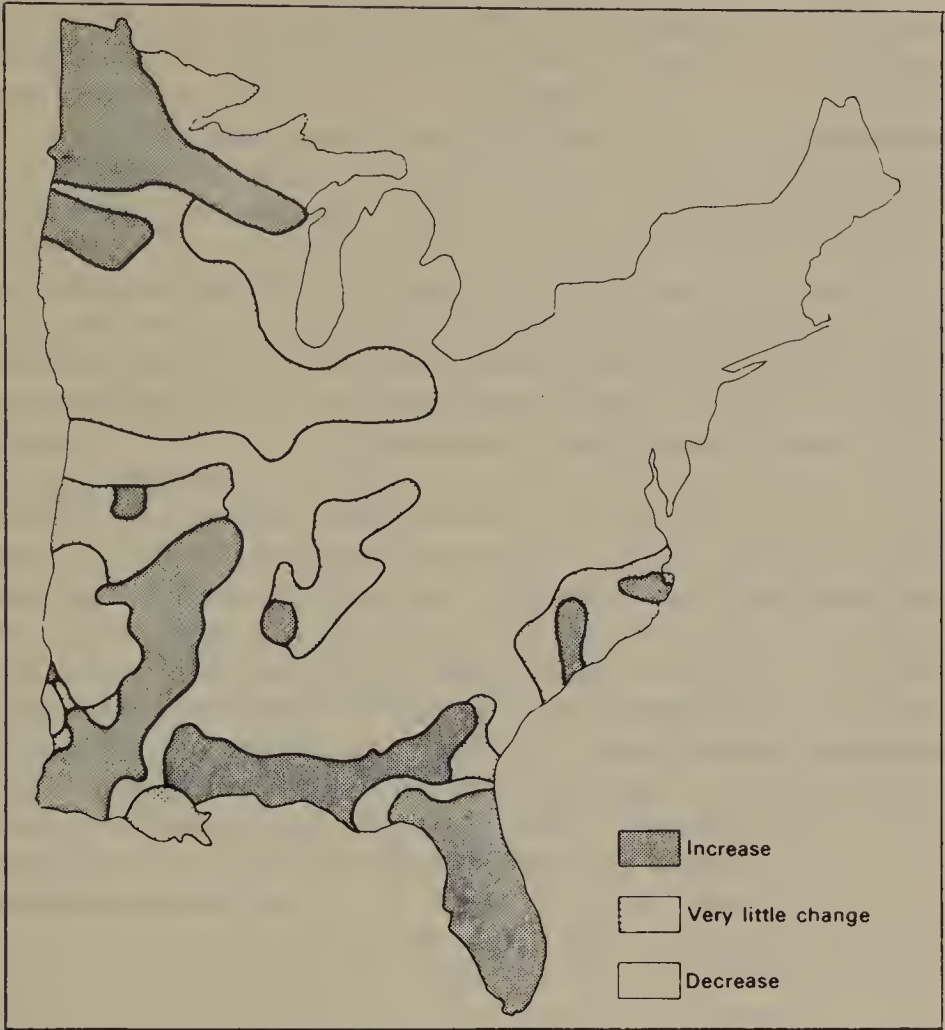
Figure 11.3 Change in cleared farmland acreage, 1910–59. (Areas generalized from Hart (1968). © Association of American Geographers.) The factors underlying change on this map are very complex and include increasing urbanization and industrialization and the building of roads as well as the abandonment of marginal farming land in the poorer soil areas in the east under competition from more efficient farming in the Mid-West.

so that their nutrient reserves were exhausted and the uplands were depopulated. The raising of their status once more to the brown earth type has been shown to be possible using only a little fertilizer initially and encouraging their colonization by deciduous trees. It is estimated that the full brown earth ecosystem could be restored in about 100 years (Dimbleby 1952).

Although some of these soils have been badly managed in recent years with excessive fertilizer dressing, compaction by heavy machin-

ery and degrading of the soil animal population by injudicious use of pesticides, the energy crisis of the 1970s has been a blessing in disguise as far as soil management is concerned. Some farmers are looking once more to the use of animal manures and the practices of mixed farming to redress some of the imbalance encouraged by freely available cheap energy, and these changes can only be to the benefit of the soil ecosystem.

Probably a greater threat to the soil is the demand for land for urban development and roads. It is probably true to say that far too little consideration is given to soil resources when making planning decisions about the designation of land use. Thus, in Britain the second Land Utilization Survey has revealed how much of the land – even with higher housing densities than during the 1930s – has been wasted by poor planning (Coleman 1977). Whether, in future, Western societies will give greater consideration to soil resources and treat them with some of the respect shown by our mediaeval forebears is dependent on soil being seen as the fundamental resource on which our human ecosystem depends, and which under-pins the whole of the rest of our activities. The prospect of the world's population doubling in the next 30 years should, as Dr Johnson said of the prospect of hanging, focus the mind wonderfully. Given adequate understanding of what nature has done for us, there is no real reason why the forests and soils of this formation-type should not continue to provide man with economic, recreational and aesthetic benefits as they have done so effectively for 6000 years.

11.5   Vegetation of mediterranean affinities

The narrow latitudinal zones between the Trade Wind belts and the zone of the westerlies on the western sides of the continents present climatic features that pose plant life very distinctive problems. Precipitation varies annually between 350 and 900 mm in these regions, with up to 65% of it falling in the form of thunderstorms or irregular occurrence, both temporally and geographically. Mean monthly temperatures in winter are usually below 15°C and up to 3% of the hours during the year are below 0°C. Thus, the most propitious season for growth is the cooler part of the year and plants must be adapted to withstand the stress of summer drought. In general, the vegetation is described as sclerophyllic woodlands (i.e. trees with small, hard leaves) and it has become clear that (a) the present vegetation of many of the regions with this climate is recently adapted

to the climate, and (b) there are considerable similarities of adaptation from region to region, illustrating well the concept of convergent evolution.

The largest area, that of the Mediterranean Basin itself, has had a long evolutionary history. The genera currently present, such as *Laurus*, *Quercus*, *Prunus*, *Platanus*, *Arbutus*, *Rosa*, etc., can be identified as present abundantly in the Lower Tertiary, when the region was dominated by an oak–laurel forest adapted to a hot, humid climate all year round. Relicts of this vegetation, now almost destroyed, existed in the Canary Islands until recent times and a clear account can be found in Walter (1984). In the Upper Tertiary, aridity seems to have developed and the area acquired elements deriving from Central Asia. During this time the rainfall regime was probably dominated by summer rains. At the end of the Tertiary, cold oceanic streams gave a more general aridity, the necessary condition of the mediterranean climatic type. In the Pleistocene, cold humid periods coincident with glacial spells alternated with hot dry periods during interglacials, and these alternations gave a distinctive differentiation to the vegetation. By the Holocene, much of the vegetation of the region seems to have been dominated by extensive evergreen oak forests, now dependent on a winter rainfall regime. In Section 10.2, it was shown how in south-west Australia the forests have been preserved in an altered rainfall regime as a result of Pleistocene climatic changes.

Although there are similarities of physiognomy in many aspects of the current Mediterranean vegetation to other areas with comparable climates (see Fig. 11.4), much of this similarity is attributable to the degradation of the climax vegetation by human beings. However, in the successional communities that have been developed, it is possible to draw parallels to other regions. First and most striking is the extensive area covered in all regions by evergreen shrub vegetation: macchia and garrigue in the Mediterranean region; chaparral in California; in Chile, a dense shrub vegetation with well scattered small trees and an abundant herb understorey; in South Africa, evergreen shrub vegetation (gynbos); and in Australia, mallee tall scrub (5–8 m) with a well developed herb cover. (The chaparral of California corresponds to the encinal vegetation of the mountains of Arizona with summer rainfall regimes.) A strongly developed mosaic structure to the vegetation is also apparent with a rich niche pattern and high biotic diversity, and with fire of major importance in determining the pattern of the mosaic. High species diversity is also notable, which is to be expected with the levels of stress from drought

and disturbance from fire (see Ch. 7), and this is particularly emphatic in areas where overgrazing occurs (Naveh & Whittaker 1979). The marked evolutionary convergence in species richness, growth form, leaf duration, leaf size (Fig. 11.4) and spininess from one area to another, although there may be no species or genera in common, is very noteworthy. California and Chile, for example, have no species and only three genera in common. Naveh and Whittaker (1979) distinguish in this respect: (a) Pleistocene communities of the Mediterranean, Chile and California, which have significant human interference allowing invasion of the vegetation by annuals, and have
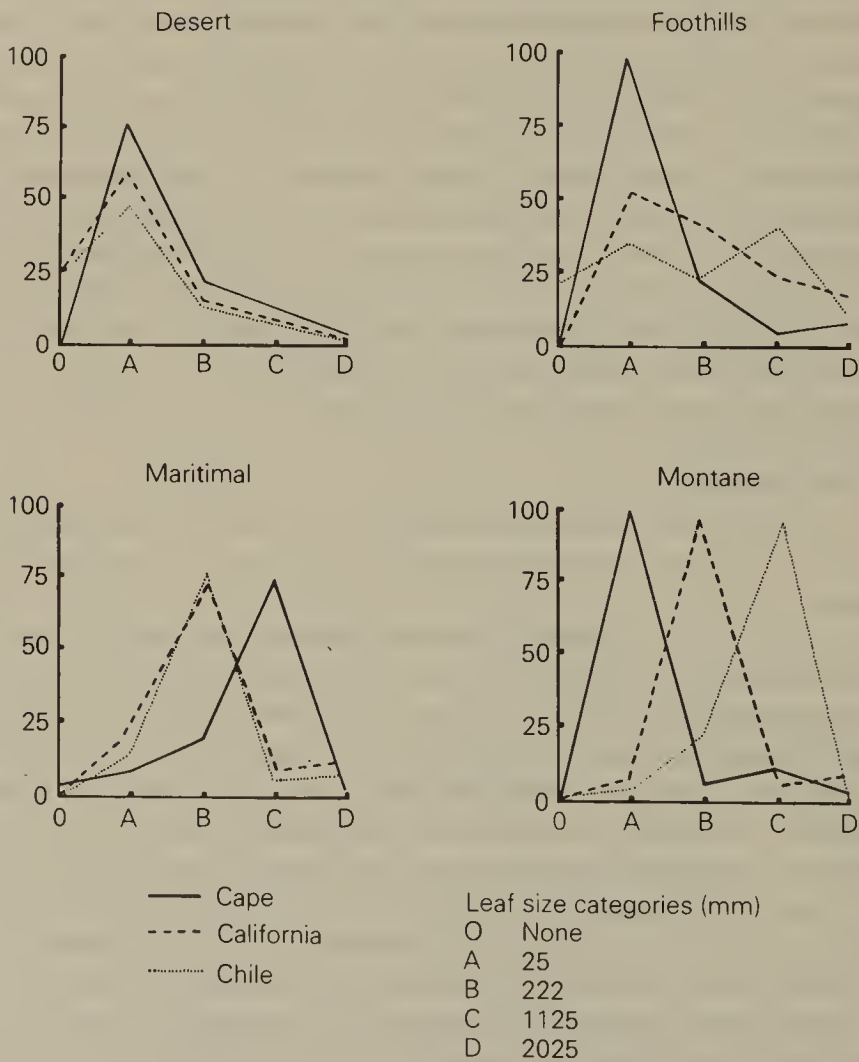
Figure 11.4 Percentage of woody trees with each of five leaf size categories at four analogous points in Chile, Cape (South Africa) and Californian vegetation. (After Cowling and Campbell (1980).)

very high alpha diversity in their communities (see Fig. 7.4); and (b) Gondwanan communities (Australia and South Africa), which are more stable and have lower alpha diversities as a consequence of more continuous evolution. Cody and Mooney (1978), in contrast, regard high diversity as a case of divergent rather than convergent evolution, while Cowling and Campbell (1980), along with other authors, conclude generally that the overall reduction of the standing crop in the Mediterranean area through grazing over thousands of years has stimulated evolution of the flora.

Pignatti (1983) has provided a large number of examples of productivity in the various forest vegetation types in the Mediterranean region, and found very wide ranges with a close relationship to soil types. On the poorest soils in Sardinia and Dalmatia, net primary production varies from 2 to 2.5 t ha^{-1} y^{-1}, although in better watered conditions on similar soils production can rise to 7 t ha^{-1} y^{-1}. Mesotrophic soils in samples from Venezia, the pre-Alps and the Dolomites, with median moisture conditions, provide sclerophyll woodland with sufficient nutrients to sustain net primary production levels of 7.5–12 t ha^{-1} y^{-1}. The eutrophic soil areas with adequate rainfall or soil moisture reserves produce the highest levels of productivity of 14–15 t ha^{-1} y^{-1}. The most important geographical region in this category is the North Italian Plain. Thus, even the most favourable conditions for plant growth fail to produce production levels matching those of the temperate deciduous forests.

Walter (1984) has clearly identified the distinctive advantages of the sclerophyllous habit in competition. Observations over the whole growing season show that osmotic pressure in the leaves rises by only 4–5 atm during the dry season, so that the hydrature of the protoplasm falls hardly at all. This results from partial closure of the stomata. Soft-leaved plants (*malakophyllous*) such as species of *Cistus*, *Thymus* and *Viburnum*, although provided with protective hairs in young leaves and buds, shed most of their leaves in the dry period, as do deciduous trees. Most evergreen trees are sensitive to drought in any case. Consequently, when water is available once more, sclerophyllous species have the great advantage of recommencing production in advance of most other types.

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12

The coniferous forests of the Northern Hemisphere

The great tracts of boreal forests of the cold temperate lands are not the only lands dominated by conifers. As Figure 8.2 shows, on the western seaboard of North America, lands with cool, very damp climates have extensive coniferous forests. In mountainous regions, the sub-alpine stages are dominated by conifers. There are extensive coniferous forests in Brazil and they are important in the Mediterranean Basin. Clearly all these types are not of the same kind, nor are they responding to the same environmental circumstances. In one formation it may be their resistance to drought that is important; in another, their resistance to low temperatures; in yet another, their resistance to fire. The characteristics are set out in Table 12.1, but it is with the best-known type, the boreal forests, that this section is most concerned.

12.1 Biomass, productivity and mineral cycles

The mean biomass of mature boreal coniferous forest seems to be around $100t$ ha^{-1}, although the range is wide, $25–175t$ ha^{-1}. The leaf portion is greater than that in the deciduous forests, and in boggy areas and low-quality open forest the contribution of the ground flora to the green biomass can be very large indeed, reaching 40% in some wooded swamps with considerable bog moss (*Sphagnum*) growth. There is some confusion as to just how great biomass can be. Rodin and Bazilevich (1967) cite well managed plantations of larch about 140 years old as having a total plant biomass of $800t$ ha^{-1}. However, natural formations are much lower than this, within a range from 80 to $300t$ ha^{-1}. Net primary production varies greatly according to age and quality of stand, species composition, climatic conditions, ground conditions and the degree of waterlogging. The range seems to be $4–20t$ ha^{-1} y^{-1}, with a mean around $8t$ ha^{-1} y^{-1}. Thus, spruce

Table 12.1 Major coniferous forest formation-types.

Type	Location	Botanical character	Environmental relationships
boreal forest	N America and Eurasia	species of pine, spruce, fir and larch plus birch, alder and poplar	vegetative life confined to four months approximately; strongly xeromorphic to withstand physiological drought of winter; deciduous larches (e.g. the Dahurian larch of Siberia) are often associated with the most rigorous conditions; local edaphic climaxes occur – for example, white spruce (*Picea glauca*), balsam fir (*Abies balsamea*) and European spruce are associated with deeper loams, the jackpine (*Pinus banksiana*) and Scots pine (*P. sylvestris*) with poorer sandy types
sub-alpine types	Himalayas, Alps, Caucasus, Rockies, Carpathians and Cascades	the genera and in some cases the species of the boreal forest	the growth season and the length and climatic severity of winter are broadly comparable to those in the boreal forest
western N American coastal forest	from Alaska to California	many species and subspecies with Sitka spruce (*Picea sitchensis*) often dominant from Alaska to British Columbia, redwoods in Oregon and N California and Douglas fir (*Pseudotsuga taxifolia*) in British Columbia and Washington	with such a span of latitude, the main environmental influences vary considerably; the distribution of redwoods, for example, can be closely correlated with fog incidence while the Douglas fir is associated with the liability to fire
montane forest of N America	interposed between coastal forest and sub-alpine types	ponderosa pine (*Pinus ponderosa*), Douglas fir, white fir (*Abies concolor*) and redwood (*Sequoiadendron sempervirens*) are the main dominants	one of the most important ecological relationships is to fire – most of the species are fire-resistant; in most of the climatic zones, strong summer drought favours the coniferous habit
lake forest of N America	Minnesota to northern New England	originally dominated by white pine (*Pinus strobus*), red pine (*P. resinosa*) and eastern hemlock (*Tsuga canadensis*)	only secondary forest remains now, so environmental relations are obscure
pine barren of SE USA	N Florida, Alabama, Texas	loblolly pine (*Pinus taeda*), shortleaf pine (*P. echinata*), pitch pine (*P. rigida*), longleaf pine (*P. palestris*) and slash pine (*P. caribenea*) dominate	forests are doubtfully a climatic climax; they may be, at least in part, fire climax maintained by aboriginal inhabitants
mediterranean types	Mediterranean Basin, California, S Chile	cedars and pines in Mediterranean Basin, pines in California, araucaria pines in Chile	all are associated with strong summer drought; in the Mediterranean Basin some of the lowland pines represent a stage towards angiosperm forests

usually displays higher net primary production than pine, but this cannot be solely ascribed to the differential capacity of the two as primary producers. As can be seen from Table 12.1, pines and spruce prefer different soil types, the spruce usually occupying the more eutrophic soils such as deep loams over glacial clays, which encourage a greater production than the more oligotrophic sites occupied by pines. Moreover, experiments in Sweden to test the response of forest trees to the effects of fertilizers showed significantly higher levels of production in Scots pine than those usual in natural conditions. The cultivation of lupins within the pine stands, for example, more than doubled net primary production in 50-year-old trees, an improvement that was sustained for at least 10 years (Stålfelt 1972).

The nutrient cycles of the boreal forests are significantly different from those of the deciduous forests. In the first place, the needles of the trees – apart from larch – are much longer-lived than the leaves of deciduous trees, and over their life they lose nitrogen and other elements by leaching. Thus, the litter returned to the forest floor has few elements that would neutralize the products of humification, and an acid humus results. The needles also carry waxes and resins, which are not readily eaten by animals or easily humified. In any case, the generally low temperatures, short active season, often poorly drained ground and low energy content of the litter inhibit the development of a flourishing soil fauna. Thus, one of the outstanding features of coniferous forest ecology is the mass of undecomposed litter on the soil surface. In the more northerly regions it may be three to five times the annual litter fall, and in swamp forest it may exceed the annual litter fall by 20–30 times. The mineral element circulated in the greatest quantity appears to be calcium. (See Figure 12.1 for pattern of circulation of this element in pine forest.)

12.2 Soil conditions

The release of acids from the litter and its poor humification and mineralization rates ensure that the formation of a stable colloidal complex with good reserves of nutrients is almost impossible. The acids migrating in the profile react with cations in the soil minerals to form complex compounds, which are leached downwards to accumulate in what is called the humus–illuvial or iron–humus–illuvial horizons (Fig. 11.2). As there is no significant upward mixing in the soil, there is an irreversible loss of nutrients, which is not fully

Note: pool and transfer values drawn to same scale
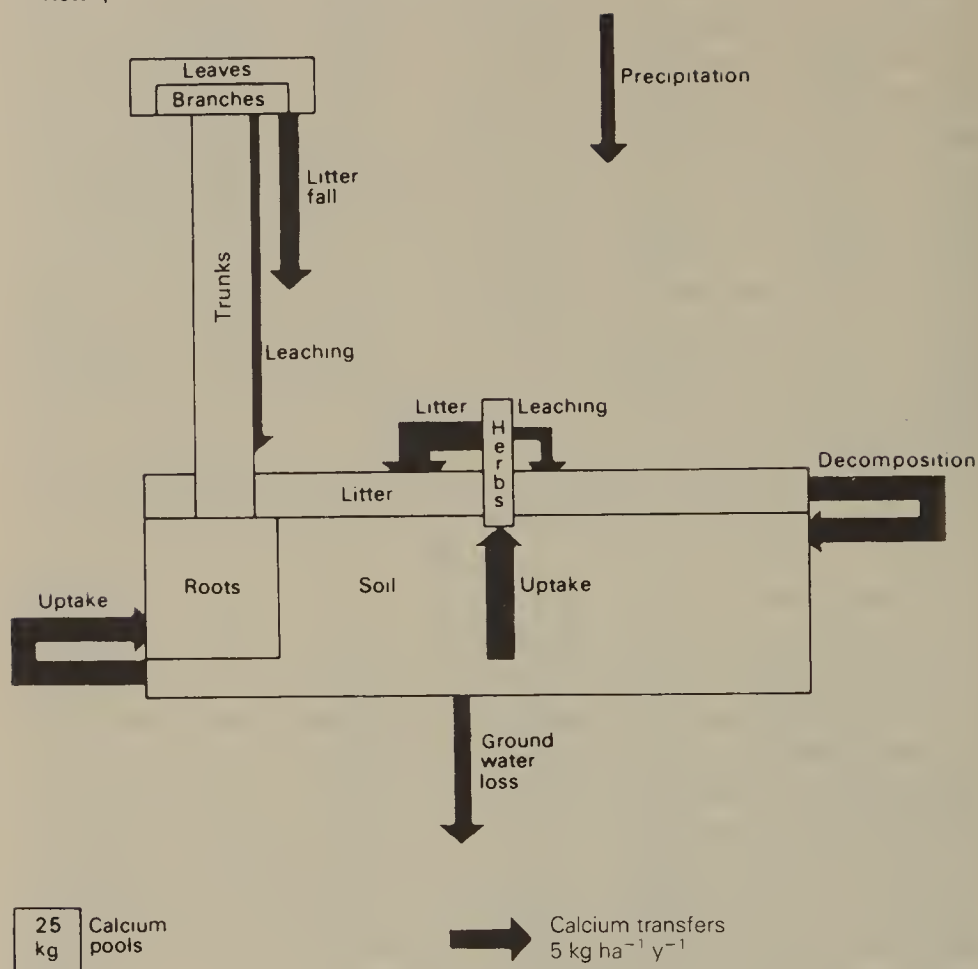
Figure 12.1   Calcium pool and transfer values for mature, stable Scots pine forest, Gt Britain. (Data from Ovington (1962).) Note that precipitation input and ground water loss are practically equivalent.

compensated for by atmospheric input or migrating birds and other animals. Given this state it is interesting to speculate whether the soil can run out of nutrients altogether. There seems to be evidence that this can happen in certain circumstances. Thus, experiments in Sweden show that, in some pine heaths, seedling growth is dependent on nutrient supply and that mobile reserves in the soil are sufficient for *only one* generation. Regeneration is only possible if this reserve is supplied by litterfall from the existing trees. If these are cut down the reserve is lost with them and regeneration ceases (Stålfelt 1972). This is an extreme case, of course. In most forests, available reserves in the soil or from ash are usually sufficient to ensure regeneration after felling or burning.

A vital role in maintaining the nutrient cycles in these forests is played by the mycorrhizal fungi. They infest the litter and ensure that the mineral elements are transferred directly to the host tree before the nutrients are leached downwards out of reach. In fact, there are many similarities in their role in these forests to the part they may play in the hot wet forests. There is good evidence that mycorrhizae represent a major pathway from litter to tree for nitrogen.

Evidence has been produced (Elliott-Fisk 1983, Scott *et al.* 1987) that there may be important changes taking place at the poleward limits of these forests. In Canada, the central regions of the boreal forests appear not to be regenerating themselves effectively so that the northern boundary is becoming unstable. At the eastern and western edges of the forest, on the other hand, stability appears to be maintained.

12.3 'Mixed' forests

The transition from coniferous to deciduous forests is very wide, so wide in fact than many authorities recognize it as a distinct formation-type, often called *ecotone mixed forests*. However, the conifers and deciduous trees do not readily form mixed stands. Instead, a mosaic pattern of distinct associations occurs, dominated by one or the other vegetation type. Thus, in European Russia from 59° southwards, on the deeper loams the spruce is replaced by the oak (*Quercus robur*), but the poorer sandy soils continue to be dominated by pines as far south as the Ukraine. Except on a very broad scale, the continuum concept of vegetation is difficult to recognize in these forests. Their pattern is much nearer the polyclimax envisaged by Tansley. A similar pattern of fairly discrete associations can be recognized in North America, where sandy outwash lands in Minnesota, Wisconsin and Michigan were originally dominated by red and white pines, while on the deeper loams oak and hickory associations flourished. In the Far East, in northern and eastern Manchuria, northern Korea and northern Japan, the flora is richer than in Europe or North America and the mosaic more complex with many more truly mixed stands.

The boreal forests represent one of the world's great ecosystems into which man has ventured in large numbers only recently, and for the most part they are still wilderness. Only in Europe and here and there in North America and the USSR have extensive inroads been made. As these formations lie almost wholly within the purview of

advanced industrial societies and a great deal of knowledge has already been accumulated about their management for continuous timber production, their future should be assured. It is probable that the enormous cost of improving their soils for agriculture to counter the impoverished nutrient cycles is likely to prevent the development of much farming, except perhaps under extreme population pressure in China and Japan. Besides which, in North America and Russia, there are still extensive lands with better soils that have not yet reached their full agricultural potential. (See, however, Azhiev (1976) for an account of damage to the Siberian taiga.)

The mixed forests, on the other hand, have been extensively cleared already in Eastern Europe and around the Great Lakes in North America and their brown earth soils especially have been made almost as productive as those in Western Europe. Some of the farming on these soils is, however, quite ancient, as in Finland where shifting burning began between 5500 and 4600 BP, and farming around 3500 years ago. Burning has significantly increased the area, even in quite remote places, occupied by several tree species (*Betula*, *Alnus*, *Pinus* and *Populus*), according to Hamet-Ahti (1983).

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13

The temperate grasslands

The majority of the lands formerly covered by the temperate grasslands are now under cultivation or controlled grazing. Only the drier edges are comparatively little affected. It is true that there are reserves in North America, the USSR and Central Asia, some of considerable size, where the ecosystem comes close to its original nature, but even here the animal populations integral to the ecosystem have been much reduced. Consequently, it might be thought that the descriptions of the ecology of these lands are only of academic interest. However, in one important respect this is not so. Many of these lands have suffered in the past precisely because of the lack of this 'academic' knowledge. Even if the species that composed the living part of the ecosystem have gone for ever, their shadow is still cast in the soil. Moreover, not only is ecological knowledge essential for the maintenance of the soil in good heart; the essential preservation of the genetic resources of the plant and animal species forms a reservoir for breeding, and a number of centres have been established for this purpose in the USA.

13.1   Vegetational features

Physiognomically, the steppes or prairies are usually dominated by more or less xeromorphic grasses with intensive rooting systems mixed with other life-forms including herbaceous annuals and perennials, bulb plants and woody shrubs. They occur under a variety of climatic regimes in mid-latitudes, all characterized by a dry season. Formations to which the term 'steppe' has been applied have also been described as occupying the Sahel zone at the southern Sahara fringe, parts of Namibia and south-west Australia. The term 'pseudo-steppe' has also been used for such formations.

  The particular structure and floristic character of these grasslands vary according to climate, soil type and biotic factors, but it must be noted that the ecological status is very difficult to determine exactly in

many cases. There is good evidence from many parts of the world that fire has had a considerable part to play in their maintenance and that much of the firing was induced by human beings.

Also, it must be emphasized that the development of any grassland is not a simple response to climate or any other single factor. Their existence depends on a 'complex of selective forces' (McMillan 1959), no small part of which was the enormous population of grazing animals that formed an integral part of the ecosystem. Moreover, the differentiation in feeding niche amongst these animals ensured that there would be few herbaceous or woody species unaffected by grazing or browsing. The populations carried by these formations, even such a comparatively short time after their demise, are now difficult to imagine. The buffalo population has been estimated at between 50 and 60 million before its decimation, each of them consuming almost as much as a cow. These animals shared the land with large numbers of pronghorn antelope and others such as the rodent 'prairie dogs' (*Gnomys*), which were organized into societies with territories covering several square kilometres. They consumed enormous amounts of plant material: for example, 87% of the total production of a steppe area studied in Arizona. It would have been a very resistant woody plant indeed which could have reached any great height in face of the irresistible combination of drought and feeding pressures.

In both Northern and Southern Hemispheres there is a change in grass families from temperate to semitropical and tropical zones. Temperate grassland genera belong to the *Festuciodeae* but subtropical and tropical lands are dominated by genera of the *Panicoideae*. For example, in the Ivory Coast savannas mentioned in Chapter 10, 77% of the grass species belong to the *Panicoideae*, the remainder being of the *Festuciodeae* with primarily tropical or subtropical distributions. In the Canadian prairies, 93% of grasses belong to the *Festucoideae*. In Australia, over 70% of grasses are genera of the *Panicoideae*, but in New Zealand the tussock grasses are overwhelmingly of the *Festucoideae* (Looman 1983).

Connor (1964) has presented evidence that the tussock grasslands of New Zealand originated through forest burning possibly between AD 400 and AD 600. The first grassland that seems to have been produced was short-tussock, progressing through snow-tussock to the tall-tussock type prevailing at the time of European settlement. European burning seems to have reversed the process back to short-tussock grassland.

The preponderance of grass species from these two families has the

corollary that certain genera are common to all grasslands in any given climatic zone. In most regions, grasslands have been classified into various types using frequently recurring assemblages of species to form 'sociations', usually named after the predominant species. Recurring combinations of plant species can, in most circumstances, be considered indicative of similar ecological conditions, even if the communities are widely separated geographically.

The dominant grasses of the northern mid-latitude steppes belong to the genera *Stipa*, *Agropyron*, *Koeleria*, *Festuca*, *Andropogon* and *Elymus* and these, with others such as *Themeda* in the South African grassveld and *Melica* in the pampas, also occur in the Southern Hemisphere. The better-watered steppes with rainfalls around 2000 mm y^{-1} carry taller grasses with deeply penetrating and highly ramified roots. In the American tall-grass prairies, the common dominants such as *Andropogon* spp. and *Stipa spartea* reach 2 m or so. With increasing drought along the moisture gradient towards sub-arid regions, the tall-grass steppe gives way to a mixed steppe of tall and low forms and finally to short-grass formations where the dominant buffalo grass (*Buchloe dactyloides*) and grama (*Bouteloua gracilis*) reach only a few centimetres. A similar gradient was originally observable in the USSR.

Reference has already been made (Ch. 3) to the ecotypical zonation into long- and short-day types of these grasses that occurs with latitude, and studies show that the apparent uniformity of the grasslands conceals the fact that they are a mosaic of ecotypic variant species. McMillan (1959) has pointed out that other ecotypic variations, for example, in relation to soil, lead to the grasslands displaying 'a geographic repetition of certain species and genera over an obvious non-uniform habitat'.

The Southern Hemisphere varieties of steppe land occur under a range of climatic regimes and are all of doubtful status as climatic climax formations. The pampas type of southern Brazil, Uruguay and Argentina, which originally displayed something of the division into long- and short-grass types, has almost entirely disappeared as the original bunch grass (*Melica* spp.) have been replaced by European turf-formers. In areas like Uruguay and north-east Argentina, with apparently more than enough rainfall to support trees, they may, in any case, have been a fire climax maintained by the original Amerindians. Similar suggestions have been put forward less convincingly for the South African grassveld. In Australia, although there were originally wide areas of grassland composed of mixed tropical and mid-latitude species, these are often continuous with the tree

savanna and the grass and shrub strata of open eucalypt woodlands, so they resemble those of the Northern Hemisphere only super-ficially.

A further dimension to the explanation of the biogeography of grasslands has been added by the examination of photosynthetic pathway in grass species. Evidence, relating in particular to grasses, has been presented that the geographical distribution of C3 and C4 species can be understood in part as a differential response to climatic conditions in plants possessing these characteristics.

There is general agreement that, in the Spermaphyta, three photosynthetic pathways exist. These are termed the Calvin–Benson or C3 pathway, the Crassulacean acid metabolism (CAM) pathway and the Hatch–Slack or C4 pathway. The pathways C3 and C4, which are overwhelmingly the most frequent, are associated with distinctive leaf anatomies, the former having the main photosynthetic tissue in the form of palisade layer and spongy mesophyll, the latter with its main photosynthetic tissue concentrated in the bundle sheaths. The significance of the discovery of C3 and C4 plants was appreciated in the 1960s in relation to the rates of photosynthesis that each pathway allowed. C3 photosynthesis is more efficient in good light and water conditions, but C4 photosynthesis is initially more rapid and can be carried on even when stomata are closed. Apart from noting the importance in some cereals of the C4 pathway, the further bio-geographical implications of C3 and C4 photosynthesis began to be examined in detail only in the late 1970s as the inventory of plants with each pathway type became sufficiently extensive.

Teeri and Stowe (1976) presented evidence on climatic factors and the distribution of C4 grasses in North America that the relative abundance of C4 species in any particular region is strongly corre-lated with minimum daily temperature during the growing season. In a comparison with dicotyledonous C4 species (Stowe & Teeri 1978) they found that the climatic preferences of the two C4 groups differed considerably, and the distribution of C4 dicotyledonous plants (dicots) could be more effectively correlated with high evapotrans-piration rates in the growing season. However, the overall continent-wide distribution of C4 dicots shows a dimunition from south to north broadly in step with the poleward temperature gradient.

Collins and Jones (1985) also show in Europe that the distribution of C4 plant types is correlated with temperature (Fig. 13.1), and in both continents the floras of the boreal forests and tundra vegetation are virtually devoid of C4 plants. Work has also been published on the distribution of C3 and C4 grasses in Australia (Hattersley 1983).
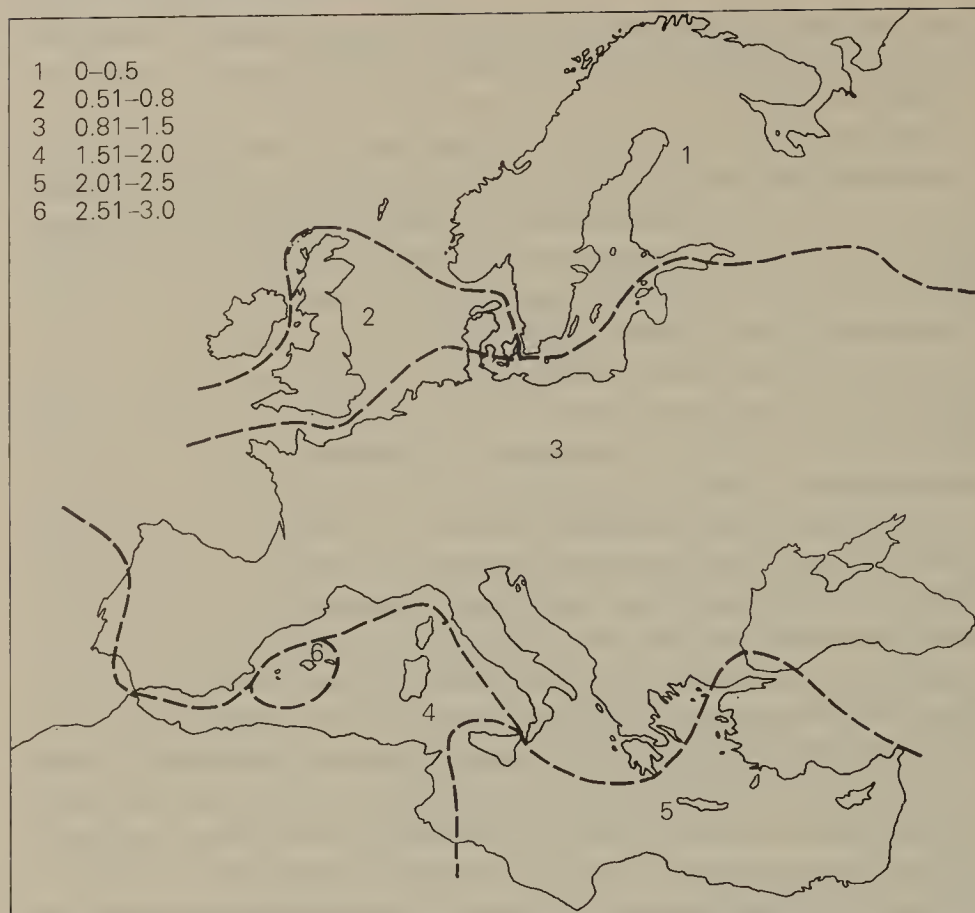
Figure 13.1 Distribution by percentage of total angiosperm flora of C4 species in Europe. (After Collins and Jones (1985).)

In lower latitudes the distribution of C4 species correlates well with aridity.

Stowe and Teeri (1978) point out, however, that there are many factors other than the particular photosynthetic pathway that affect whether or not plants can become established. As they make clear, introduced C4 plants in North America show little or no correlation in their distribution with climate.

13.2 Biomass, production and mineral cycling

Total plant biomass lies in the range 20–50t ha^{-1} for what Russian authors describe as 'plakor steppe', i.e. flat or slightly undulating, well drained grassland above valleys and ravines. Although consider-

able variation occurs from year to year according to wetness of the season, the total plant biomass remains constant overall. This is due to the carry-over from one season to another of root material whose decay is greatly reduced in dry years. Total net primary production varies between about 1.5 and 15 t ha^{-1} y^{-1}, with a mean around 5 t ha^{-1} y^{-1}. As in the savanna, production is closely related to rainfall, but within quite short distances the vegetation mosaic produces surprisingly high variations. In North Dakota, for example, the tall-grass type has three times the production of short-grass association nearby (Hadley & Burcos 1967). Data from the USA and USSR show that biomass varies very little from one steppe to another. Along the moisture gradient from wet to dry lands, the falling proportion of above-ground material is balanced by the increase of root material.

In an ecosystem dominated by herbs, the litter amounts are naturally very great, usually over 40% of the total above- and below-ground organic matter. The amounts of nutrients – especially silicon, nitrogen, calcium, potassium and phosphorus – returned to the soil are considerable. In fact, the long-grass prairie (steppe-meadow) returns the largest amounts of nutrients to the soil annually of all the temperate vegetation types. The rate of decomposition is usually somewhat slower than its supply, so most soils have a thick sod or 'steppe matting' several centimetres thick whose mass is usually larger than the total mass of the above-ground green parts. The amount of matting varies from season to season but always exerts a considerable effect on the soil moisture balance. It interferes with percolation and intercepts and holds water that falls onto it. As evaporation rates are highest in the rainy season (summer) little downward percolation takes place and much of the water that finds it way into the soil is from melting snow. Consequently, the subsoils of the steppes tend to be very dry, some of them almost permanently so. In moister regions, snow-melt and heavy summer storms do produce downward movement of the most mobile soil compounds, for example, sodium and potassium salts. In the *prairie soil* type of the USA, the amount of leaching is sufficient to produce a slightly acid reaction.

Steppe matting is also effective in preventing erosion. Water-wash is prevented and so is wind-blow, as the fine, often silty, particles characteristic of the soils are never in direct contact with the atmosphere. Where matting is removed by ploughing or overgrazing, its protective function has to be compensated for in some way, for example by mulching (i.e. covering the soil with straw and leaves), by

wind-break planting (as in the southern Ukraine), by contour ploughing or by combinations of techniques suited to local needs.

13.3   Soil types

Three widespread major soil types are associated with the temperate grasslands of the Northern Hemisphere, and their main features are set out diagrammatically in Figure 13.2. The processes that result in one of the most characteristic features of these soils, the accumulation of lime, are explained in Figure 13.3.

When men first broke these soils with their ploughs, the initial high yields were sometimes followed by widespread soil erosion by wind and water. In the USA in the 1920s, in Australia in the 1940s and in Kazakhstan in the early 1960s, disastrous losses of soil occurred because land management practices ignored the realities of ecology. In America, studies by ecologists, agronomists, hydrologists and engineers have gradually built up adequate measures for conserving the soil in good heart, and these are embodied in the work of the US
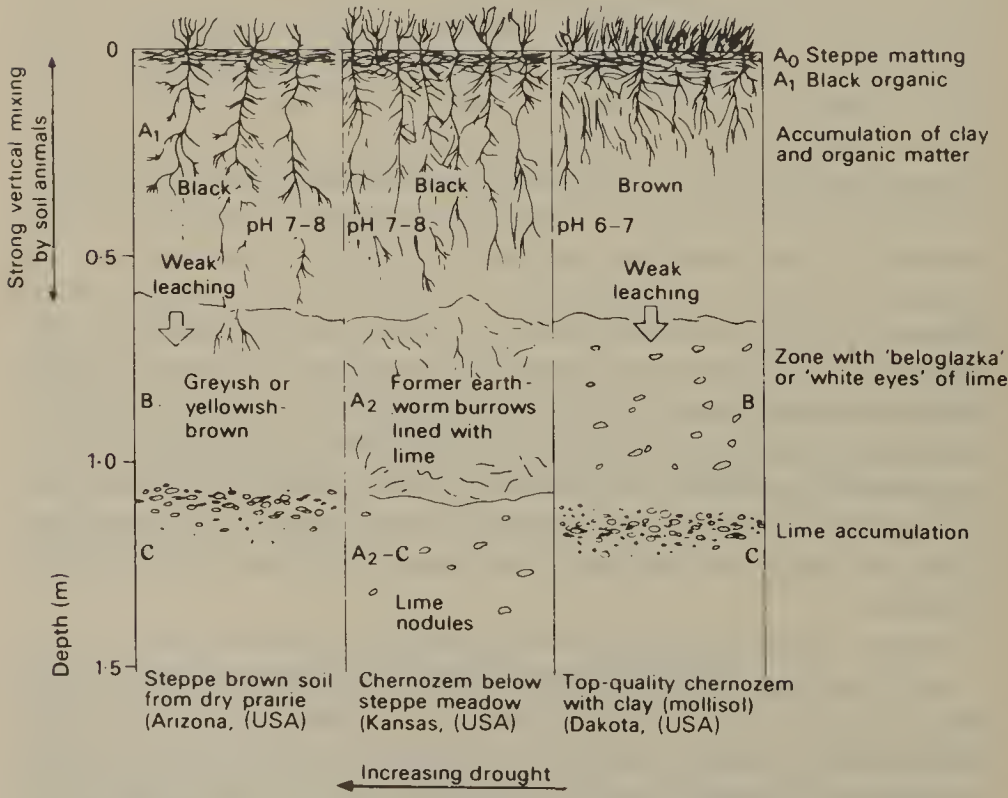
Figure 13.2   Steppe soil profiles.
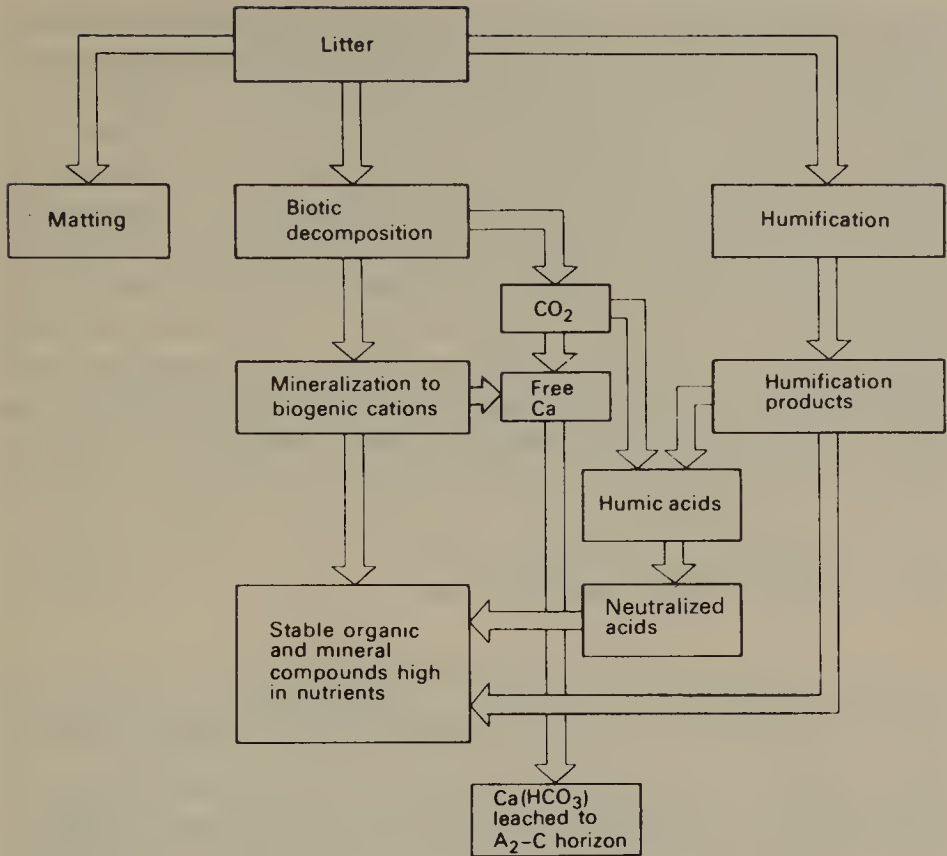
Figure 13.3 The process of litter decomposition in chernozem soils.

Soil Conservation Service backed by the power of federal law. By the early 1950s, over 75% of the arable lands of the USA were covered by strict federal conservation laws. The tragic loss of soil from the plains of Soviet Central Asia in recent years occurred precisely because the lessons learned at such painful cost in terms of human misery and dollars in the USA were not heeded.

Although the great herds of these plains have gone for good, the soil populations are still there, and so in the drier edges of these lands are the plant species. As part of the management of these lands in the USA, breeding programmes are encouraged to improve the range plants particularly. These programmes represent a model for many ecosystems in the future. The fact that the USA has turned what, only a few decades ago, were virtual disaster areas into some of the most productive land in the world shows what can be done, given political will allied to scientific resource management.

That such practices should incorporate, as an integral part of their activities, the conservation of genetic material is an increasingly

urgent need in all parts of the world. In the 1920s the great Russian botanist N. I. Vavilov mapped the homelands of many of our major crop plants and traced their lineage to their wild ancestors (see Vavilov 1952). Recent studies show that many of these wild ancestral types are rapidly disappearing. Once lost, their genes are lost for good and the highly bred food plants cannot be back-bred with the wild types, which may contain just the genes required to cope with environmental hazards like disease or low rainfall. The proposal to establish plant gene banks under the aegis of the FAO has been enthusiastically received, and the model for such banks has been established in Italy at Bari. In the next decade or so the needs of the world for a network of such stations will pay handsome dividends on the modest investment involved (Heslop-Harrison 1974).

13.4   The grassland–forest ecotone

The junction of grassland and forest in the temperate latitudes is one of the most complex and interesting transitions of any amongst the world's vegetation types. It is also one of the most puzzling. From some accounts it was possible in places to walk from closed forest to open grassland in the space of a few yards. In other places, islands of forest existed out in the open prairies and the patches of grassland amongst the forest created a park-like zone tens of miles deep.

Many workers have advanced hypotheses to explain the intricate nature of this **ecotone** and most are agreed that a simple climatic explanation is unsatisfactory. Fire and human interference have undoubtedly had some influence, but these are insufficient by themselves to account for the characteristics of the transition. In the Canadian park zone, for example, the aspen is fire-tolerant and can reproduce by suckers. Also, in Alberta, the Ukraine, the Danube Basin and European Russia, relict chernozem soils (called *grey-brown forest soils*) exist under closed forest, indicating invasion of former grasslands by trees. Why this happened is impossible to say. In America it certainly took place before European settlement. Extreme views as to the anthropogenetic origin of grasslands are hard to sustain in face of (a) the fact that steppes have been features of the world's vegetation in epochs other than the present interglacial (Fig. 2.9) and (b) the evidence that the community structures of the Northern Hemisphere grasslands are so complex and well integrated that they are hardly likely to have come together by chance. In the view of some ecologists (Walter 1984), trees of the temperate lands –

as successors to the Arcto-Tertiary forests – are all of closed forests and cannot possibly maintain themselves in competition with grasslands without the preceding successional stages to closed forest. In this view it is these preceding stages that are likely to be least successful in competition with grasses. Yet in Canada, the aspen succeeds in establishing itself very well. Perhaps as these lands become further incorporated into farming systems this problem is destined to become one of the great unsolved puzzles of biogeography.

As Looman (1983) states in a comprehensive review of the impact of people on this ecosystem type, it is quite impossible in the temperate grasslands to decide what is 'natural' and what is 'semi-natural'. (See also Walter (1984) on the evolution of grasslands in South America, and Axelrod (1985) and Whitford (1983) for accounts of the evolution and fluctuation of grasslands in North America.)

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Part 3

The vegetation of extreme habitats

14

Adaptations and selective factors: an introduction

The limits of the habitable Earth for terrestrial green plants are presented by environments where temperatures are too cold at high latitude and high altitude, where there is chronic aridity and where the land meets either salt water or permanently flooded ground. The particular stresses that these environments impose on plant life have been strong selective forces in evolution, so that highly specialized kinds of vegetation have developed with many adaptations of physiology, morphology and community structure to enable them to survive and flourish. In the last respect, for instance, dominance by a single genus or species in most benign environments is unusual; but in extreme environments, dominance by a single or very small number of plant types is a fairly common feature. The following brief examples illustrate the far-reaching adaptations that may be involved in effecting this dominance.

The genus *Potamogeton* (pondweed) is a widespread and successful plant, dominating extensive stretches of the lake-littoral environment in many parts of the world. The species of this genus all have abundant protein content yet they are not consumed by aquatic fauna. Research reveals that they have a strong defensive mechanism preventing grazing, namely the alkaloid content of their cells. In one study of nine species, almost no alkaloid present was found in common amongst the species studied yet all the alkaloids were equally effective grazing deterrents (Ostrofsky & Zettler 1986). It may be expected that a search for a similar physiological defence mechanism in other unconsumed aquatic plants would reveal these also.

In other extreme habitats, the stresses imposed on plant physiology can generate actual stress metabolites. These, in turn, may become selective factors. For example, Smirnoff and Stewart (1985) suggest that sand-dune plants generate chemicals in relation to water and salt stress and that these may confer advantages to the dune plants in giving them protection against heat damage during drought. (This

work could be of wider applicability to hot desert plants as a whole, although there is no direct evidence as yet. (See Osmond *et al.* (1987).)

Some of the most severe difficulties for plant growth of all the Earth's environments are encountered in high mountain habitats. In almost every aspect of growth conditions, i.e. water balance, temperature, wind and above all the nature and intensity of radiation, severe stress is involved (Terjung *et al.* 1969). The last factor is potentially very damaging. To survive at high altitude, all green plants must be adapted to resist the incidence of high-intensity ultraviolet radiation, which has the potential to destroy protein structures and so interfere with physiological processes, in particular the basic photosynthetic pathway. As outlined below (Ch. 17), the selective effect of this factor has been clearly shown by a number of studies.

Although high mountains, subglacial lands, shores and deserts represent the limits of tolerance of land plants as a whole, it should not be forgotten that any particular species at the limits of its geographical range is subject to environmental stresses which *to that species* may be qualitatively similar to those encountered by the vegetation of extreme habitats. However, unlike the vegetation at the extremities of the habitable land, the degree of adaptation at the limits of tolerance for most species is determined more by the area of its optimal habitat than by its limiting one. For species at the limits for plant growth as a whole, it is the adaptation to the limitations that makes them successful.

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15

Vegetation of arid lands

15.1 Locations and characteristics

According to Unesco's Programme for the Arid Lands, areas that suffer from lack of water throughout the longer part of the year cover some 35% of the world's land surface (Fig. 15.1). However, to define them precisely is not easy. Rainfall alone cannot be used, as they cover tropical and temperate lands with very different evaporation rates. The various indirect criteria that have been proposed – the presence of lakes with no outflow, intermittent streams, the presence of saline areas – are not particularly satisfactory either. Moreover, at least four kinds of arid climate can be recognized:

(a)   winter rain and summer drought climates (parts of the Middle

Figure 15.1 The world's arid lands according to Unesco. (1) Extremely arid lands: true 'deserts'. (2) Arid lands: regions where aridity poses serious limitations to farming and normally only grazing is possible. (3) Semi-arid lands: regions where plough farming is possible but requiring specialized techniques for water conservation or irrigation. Note that the vegetation of the semi-arid regions would usually be classified into a number of formation-types, for example savanna, steppe or seasonal tropical forest.

East, the American south-west and the northern Sahara);
(b)   summer rain and winter drought types (central Australia, the southern Sahara, the northern Atacama);
(c)   climates with two rainy periods or no definite rainy period (south-west Africa); and
(d)   regions of extreme aridity with long runs of rain-free years.

The Unesco definition allows only the last category to be classed as true 'desert' and, although the word may be used in many parts of the world for generally arid lands, many of these 'deserts' would be excluded from this definition. Thus, it can be seen from Figure 15.1 that no true deserts are recognized in Australia, although the map of that continent is liberally scattered with named 'deserts'.

Batanouny (1983) has defined three desert types in relation to water supply to plants: (i) the accidental type, where rainfall is not an annually occuring event; (ii) the restricted type, where rainfall is annual and permanent vegetation confined to restricted areas (depressions, wadis, runnels) with relatively adequate water available from runoff and water-borne sediments; and (iii) the diffuse type in less arid areas, where the vegetation is more or less evenly distributed.

In spite of low rainfalls and high evaporation rates in all the areas marked in Figure 15.1, plants manage to survive in nearly all these lands in one form or another. A primary distinction that can be made amongst these plants is between those surviving as permanently rooted species (the perennials) and those surviving adverse conditions as seeds (the annuals). With the exception of those plants that rely on dewfall or frequent fog, most perennials have water within range of their roots. The annuals, on the other hand, complete their cycle within a very short time while water is available.

The community patterns displayed by perennial species are closely related to available water. Thus, in the transition from wet to dry areas, the rule is usually for plants to become increasingly contiguous in their distributions. They would be found clustering in hollows or other sites where runoff is concentrated. Where the land is very flat with few hollows or runnels, flood-sheets may occur (slopes as low as 1 in 2000 are sufficient), and perennial species usually increase in frequency in the direction of flood movement. This results from the fact that, the longer the sheet covers the ground surface, the more water is able to penetrate the ground.

The annual species, with their rapid germination, growth and flowering, are not exempt from the rules of plant community

development simply because their season is so short. For example, germination is often temperature-dependent, and if rain comes at the wrong time of the year many species will remain dormant whereas others may germinate. Once germination has taken place, there is often intense competition for scarce resources. Thus, if the upper soil layers are liable to dry out quickly, the more xeromorphic types are liable to dominate; but if water is relatively freely available, the less xeromorphic plants tend to be more important. Also, if there are dry spells within any rainy season, those annuals able to resist the drought are likely to be the survivors.

15.2   Biomass, production and mineral cycles

The distribution of biomass in arid conditions is mainly underground (see Fig. 15.2), to the extent in some communities of more than 80% of the living material. The green parts can be as little as 1% of the
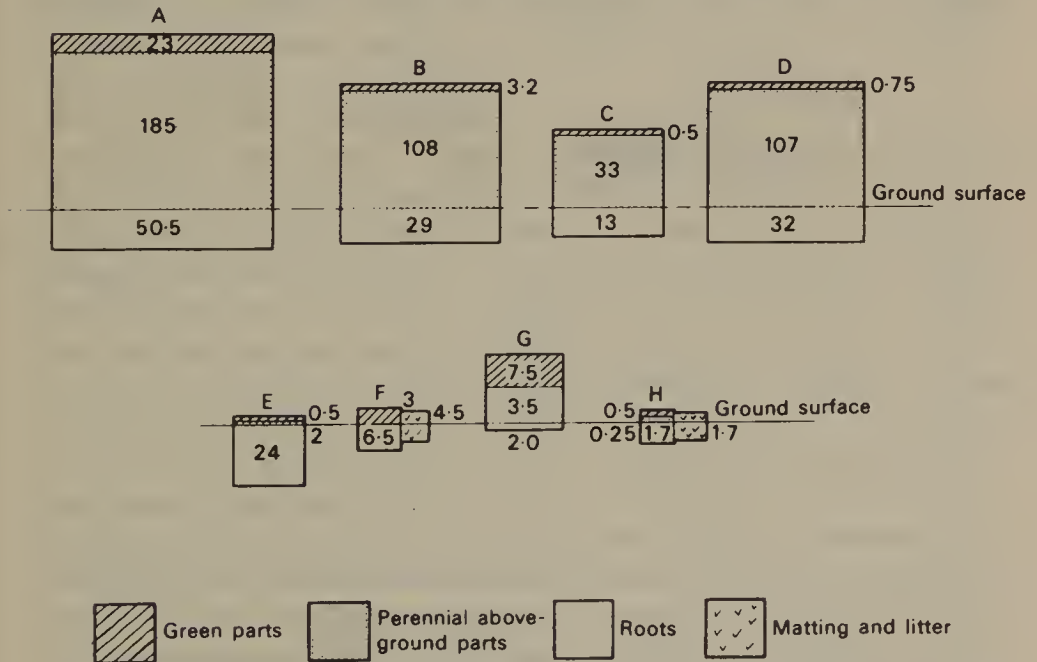
Figure 15.2   Amounts and distributions of organic matter in plant biomass in selected vegetation types (logarithmic scale). (Data from Rodin and Bazilevich (1967). (A) Tropical lowland rainforest (mean value). (B) Hornbeam forest, Crimea, USSR. (C) Birch forest (42 years old), Great Britain. (D) Green moss spruce forest (73 years old), Velikiye Luki Province, USSR. (E) Woody desert vegetation, old Anu-Dar'ya delta, USSR. (F) Steppe meadow, western Siberia. (G) Bog moss (*Sphagnum*) upland moor, Novosibirsk Province, USSR. (H) Arctic tundra communities (mean value). All figures in t ha^{-1}.

total in shrub communities, although it would be a higher proportion
where annuals are conspicuous. Annual net primary production is
very closely related to rainfall. Below a mean annual rainfall of 80
mm, the mean rate of fall in production per 10 mm of rain is about
200 kg ha^{-1} y^{-1} (Walter 1984). However, if plants are tapping
imported sources of water underground via an aquifer – the classic
Saharan oasis – or along a river, production levels can be quite high.
The *tugai* formation of Central Asia (forest–shrub–grass communities
along rivers) have levels of production comparable with those of
temperate deciduous forest. In extreme deserts, net primary produc-
tion is usually less than 50 kg ha^{-1} y^{-1}.

It is difficult to give a generalized picture of mineral cycles in arid
regions as these are so varied in type. In any case, the main part of
the essential elements is returned to the soil via root material
(80–90%), which is difficult to measure. Apart from tugai, it would
seem that nitrogen is prominent amongst the elements returned in
most communities. However, where succulents (cactus, etc.) form a
prominent feature of the permanent vegetation, there are consider-
able amounts of chlorine, sodium and sulphur returned to the soil.

15.3   Soils of the arid lands

In spite of their low production, the soil-forming processes of deserts
are just as dependent as in the better-watered lands on the cycling of
mineral elements. In very arid areas (category (d) in Section 15.1)
there are rarely any surface mantles that can be described as true
soils. However, if regular seasonal rains occur, there are usually soil
mantles.

A major distinction that can be made is between those soils which
are freely drained and those which are not. Most of the former type
under scrub are light brown or grey with little material supplied by
the vegetation, which has poor humification and mineralization
characteristics. Where grasses are dominant, these soils have a higher
humus content and often a reasonable crumb structure with a
significant biomass of soil animals. Most freely drained arid-land soils
contain a gypsum or lime horizon, which may emerge locally with
greater aridity at the surface as 'caliche' (North America) or 'tosca'
(Argentina).

On land with impeded drainage, semi-shrub and shrub communi-
ties with annual herbs are typically underlain by *sierozems*. These
usually exhibit sod formation and are constantly restructured by the

roots of annual species, rodents and insects. Litter is usually rapidly mineralized but only small amounts of humus are produced. In subtropical deserts, iron, aluminium and calcium are often mobilized and assimilated and cycled by the plants, and their reaction with the soil acids (especially iron) results in ferruginization, producing the characteristic reddish pink of the soils (Rodin & Bazilevich 1967).

Common salt often accumulates in soils in arid zones. In some areas, for example Lake Eyre (in South Australia) and around the Caspian Sea, the salt has been derived from the evaporation of sea water; but in other lands, as in Central Asia, central Australia or the western USA, the salt has been imported from the sea via rainfall.

The very arid lands with their scarce skeletal soils are usually associated with a very few characteristic species, depending on the part of the world in which they are located. In the Sahara, for example, the dune lands (erg) are dominated by the drinn grass (*Aristida pungens*) and a legume, the retam (*Retama taetam*). In the rock and stony deserts (hamada and reg), there are large tracts with no vegetation at all, plants being confined to soil pockets where grasses of the genus *Aristida* and woody plants belonging to the Chenopodiaceae can survive. Here plants may have to rely almost entirely on dewfall. In slightly saline conditions, species of the *Tamarix* and *Nitaria* occur. The fact that plants can survive at all in some of these locations is testimony to the persistence and durability of living matter against almost impossible odds. In some of the most difficult locations of all, where manganese coats the rocks, giving them a dark, heat-absorbing surface, temperatures at the hottest parts of the day reach well beyond the lethal temperature of living matter, yet plants and animals survive even here. In relation to the often enormous diurnal temperature changes to which desert surfaces are subject, it has been shown that the shade provided by perennial species is extremely important to the successful establishment of seedlings. For example, Nobel and Geller (1987) demonstrated in Californian bunch grass communities that the maximum soil temperature decreased by 2°C for every 10% increase in shading and that seedling distribution in wetted soil closely reflected this factor.

15.4 Man and the arid lands

Although the world's deserts support very low populations, the scarcity of their vegetation and its low productivity make them very liable to damage by any mishandling. In the Sahara, for example, the

grazing herds of the nomads and their cutting of wood for fuel have
easily demonstrable ecological effects, which are greater than simply
the removal of plants. Where plant cover is markedly reduced, it has
the effect of lowering the water table and increasing the soil drought,
so that once-fertile oases may be made completely useless. At the
southern edge of the Sahara, where it impinges on the semi-arid
region of the Sahel zone, the practice of burning is common as a
method of land clearance. The loss of soil moisture once the woody
plants are killed may have resulted in a measurable advance of the
desert.

For some there has been considerable speculation as to how far and
how fast the arid zone is extending and what role man has played in
this. There is some evidence to suggest that the process is part of a
world-wide change of climate, which began some decades ago, but
whether man has accelerated a process that was inevitable anyway is
not easy to say. Some American authors have speculated very freely
on this subject, but the amount of hard evidence is limited (Glantz
1977, 1987).

Undoubtedly the deserts can be made to bloom with irrigation but
it is essential to remove the salt in some way before the land can be
used. If the salt is simply washed out by excess irrigation water, the
soil may lose its structure and become poisonously alkaline. The
Punjab and the Imperial Valley of California have suffered in this
way. Techniques developed to avoid this include heavy dressings of
lime or gypsum before irrigation water is introduced. As the sodium
is lost, its place is taken in the clay–humus complex by calcium,
improving its structure considerably. Many authors have seen the
deserts with their high available energy as providing the potential
new land for cultivation of the food crops that the world will need to
support its rapidly increasing population. Various proposals have
been put forward involving the desalination of sea water (using solar
energy, atomic energy or freely available oil supplies), the importa-
tion of irrigation water from surrounding better-watered lands or the
exploitation of underground aquifers to solve the primary problem of
water supply. The enormous capital expenditure and technical exper-
tise that these schemes would require, however, might be more
fruitfully directed to better-watered lands that are undoubtedly
capable of greater production than at present. Only in the newly rich
Middle East or parts of India and Pakistan are conditions favourable
at present for extensive colonization of the desert lands, and to see
the rest of the world's deserts as a panacea for the world's problems is
yet another of the mirages that in popular Western mythology are
associated with deserts.

With increasing population pressure, these delicate ecosystems have been seriously degraded, especially in Africa, and biologists and agronomists have paid close attention to the potential crops that could be carried by arid-land agricultural systems. Many non-domesticated species have been identified which offer considerable possibilities. (For details, see Hinman (1984) and Wickens *et al.* (1985).)

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16

Wetlands

Although perhaps not so extreme in growth conditions as habitats at the marine limits to land-plant growth, nevertheless permanently waterlogged land or surface freshwater bodies present terrestrial plants with habitat conditions in which a considerable degree of specialization is required to ensure successful growth. Various terms exist to describe land where the water table is permanently at or near the surface: marsh, fen, bog, swamp, moss, mire (moor in German) and a number of local terms are frequent in both the literature and common usage. Waughman (1982) has attempted to bring some precision to this confusion by grouping the terminology into three general categories: *bog*, where water is nutrient-poor; *fen*, where water is nutrient-rich (both developed over peat); and *marsh*, where peat is unimportant. Table 16.1 sets out some of the terminology and other details, and Figure 16.1 shows areas of wetland in Europe.

The uses made of wetlands vary widely. Ombrotrophic bogs with low nutrient content and highly acid conditions are not the most hospitable substrates for agriculture. In New Zealand, they have been widely used for cranberry (*Vaccinium macrocarpon*) cultivation, and on reclaimed bogs in northern Honshu and Hokkaido islands in Japan, some bogland is used for rye and other cereals as well as root crops. Cereals and root crops are also produced from drained acid bogs in Finland, Poland and the USSR. In Fennoscandia (especially Finland, where over 30% of the land is peat-covered), they carry extensive semi-natural and plantation forests, although extensive drainage and fertilizing are necessary to encourage the growth of spruce (*Picea* spp.) particularly on these surfaces. *Pinus*, birch and alder species are more tolerant of the acid, boggy soils and are the natural colonists of raised bogs where drainage is sufficient to allow aeration so that roots and mycorrhizal fungi can become established.

In many northern European countries, peat is cut for domestic fuel, and in Ireland it is exploited on a large scale as a fuel for electricity generation.

Table 16.1 Typology and vegetation of bogs.

	Typology	Vegetation
ombrotrophic mires	upland and lowland areas of impeded drainage and lakes where bog grows above water level; may develop into *domed raised mires*; *lagg* or lateral surrounding drainage is characteristic; *aapa mires* or *string bogs* occur polewards of the raised bog zone and consist of peat running at right angles to the slope in parallel ridge-and-hollow form, the hollows having minerotrophic water, which pushes peat when frozen into ridge form; *blanket bog* (*thermal blanket mire* in Canada) occurs where mires coalesce; *transition mires* occur where there is nutrient input from surrounding mineral soils; *palsa* bogs of the peat hummock tundra are formed partly as a result of ice expansion; *tropical ombrotrophic mires* are usually domed in form	*Sphagnum* species (bog mosses) have characteristic locations, e.g. *S. cuspidatum* in pools, *S. fuscum* on hummocks; these plants have numerous empty cells, which absorb water; sedges (*Carex* spp.) and a few other flowering plants occur in the dampest conditions; in less damp areas heath plants, e.g. *Calluna vulgaris*, *Vaccinium* spp., can be found; in North America, *Ledum groenlandicum* and *Kalmia* spp. are typical; cotton grass (*Eriophorum latifolium*) and other plants occur with less oligotrophic conditions; insectivorous plants (*Drosera* spp., *Pinguicula* spp.) occur in poorest conditions; most plants display xeromorphic features; tropical ombrotrophic mires carry woody vegetation from most of the important rainforest families, and many form xeromorphic features; insectivorous pitcher plants (*Nepenthes* spp.) occur in central cupolas of raised bogs
fens (rheotrophic mires, valley bogs, minerotrophic mires)	*fluvial fen* occurs where water moves below the surface; *turf fen* occurs where water flows at the surface; fen sections frequently show that peat/water level maintains a near-constant balance over time due to water level rising as peat grows and acts like a sponge; seasonal low water stimulates aerobic bacterial decomposition, so peat is usually more degraded than ombrotrophic type	dominated by plants of the early stages of hydrosere development either floating or weakly rooted; deeper-rooted plants develop as water level falls below the surface either seasonally or permanently; the division into fluvial and turf fens is not precise and many fens are transitional, these having the richest floristic composition; where fen is invaded by trees and woodland develops, the term *carr* is employed in Britain
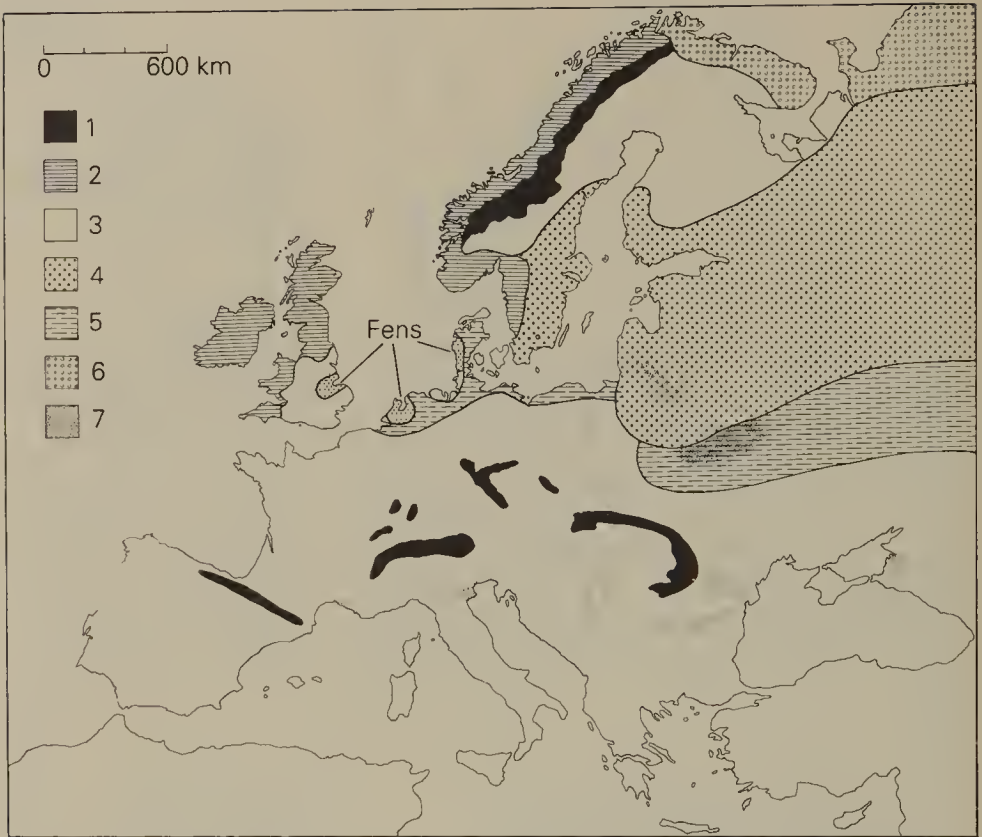
Figure 16.1   Bog, marsh and fen in Europe. (Bogs from Walter (1984).) (1) Mountain bogs; (2) blanket and raised bogs; (3) aapa bogs; (4) typical raised bogs; (5) forest raised bogs; (6) palsa bogs; (7) marshes.

Fenland in Britain and the Netherlands has been extensively drained and reclaimed from the 16th century. In East Anglia, cereals, root crops and vegetables are produced. However, the exposure by arable farming of the friable fen peat has led to extensive shrinkage as the peat dries out. It is consumed by bacterial action and also eroded by the wind. In some places the peat has gone altogether and the clay base is exposed, with old tree stumps, which represent the landscape before the marine transgression of pre-boreal times impeded the drainage.

In the Netherlands, much of this shrinkage has been avoided by concentrating on pastoral farming so that the surface layers remain covered throughout the year.

The distinction between ombrogenous peat bogs and fen peat bogs can be maintained in tropical lands, although both types are less extensive than in higher latitudes. The ombrotrophic mires are by far the most extensive and in some areas cover significant tracts of land.

(Less than a century ago, tropical peats were thought not to exist at all.) They have been recorded widely in South-East Asia, tropical Africa and South America, and there are undoubtedly many other tropical ombrotrophic bogs awaiting discovery in these lands. Detailed studies are derived largely from those in Sarawak, Borneo and Sumatra. Unlike the ombrotrophic mires of temperate lands, the peat of tropical lands is a semi-liquid mass of the remains of woody rather than herbaceous vegetation, which in any case is a very minor part of the community. Also, most of the bogs display a concentric zonation of forest communities, the central dome (cupola) often having a park-like appearance. As with temperate bogs, insectivorous plants (pitcher plants) make their appearance and are more frequent towards the bog central zone. Also increasingly towards the centre, the trees and shrubs display xeromorphic features, a characteristic of these plant communities for which there is at present no adequate explanation.

Much of the origin of these tropical raised bogs is obscure. For example, they are found often close behind mangrove vegetation, and coring reveals that the basal layers of the bogs contain mangrove wood and mangrove soil remains. Thus, a nutrient-rich habitat has been followed by and converted directly to one that is nutrient-poor. How this comes about is not well understood. The tropical raised bogs can be used for agriculture, as demonstrated in the Malayan Peninsula, where the pineapple has been successfully cultivated for over 50 years on cleared and drained bogland.

Tropical fens are rarer than tropical ombrotrophic mires, as high temperatures encourage the rapid decomposition of plant remains should water level fall seasonally, allowing the surface to dry out. Where they have been found in valleys in Africa, Malaysia and the Americas, the peat is thin and, in many, herbaceous plants contribute to their formation, for example, the common reed (*Phragmites australis*) and papyrus (*Cyperus latifolia*). At higher levels, for example in Uganda and Kenya on the East African Plateau, the lowered temperatures allow significant thicknesses of fen peat to develop and new plant types become important, for example *Osmunda regalis*, the royal fern. (*Papyrus* does not grow above 2000 m.)

Non-saline marshes are differentiated from bog and fen as they have little undecomposed organic matter in the soil. Unlike the bogs and fens, they can develop in almost any location with a near-surface water table present either permanently or for a considerable part of the year. In both temperate and tropical lands, the plant species associated with marshes are virtually the same as those of fenland.

The most striking marsh complexes are developed in areas of indeterminate drainage or where rivers carrying heavy volumes of silt meet the sea in deltas. Those in the first category in Europe and North America (for example, the Pripet Marshes of the Russian–Polish borderland, the Great Lakes area, and New England), result from the confused drainage patterns consequent on Pleistocene glacial deposition. Altered hydrology during glacial times also produced extensive deposits of valley-floor debris, and probably contributed to the enormous size of many of the deltas of the world's great rivers. Most contemporary rivers are ill-adapted to drain effectively the lowest alluvial sheets and interdistributary sites, so many major rivers developed enormous tracts of marsh along their banks and in their deltas. A good deal of these marshes have been converted to agriculture, for example in the Californian Central Valley, the Nile, the Po Valley, the Ganges and the great Chinese rivers, but many still remain, for example those of the Niger, the Parana and the Orinoco.

In parts of the tropical world such as the Matto Grosso in Brazil in the area where the Amazon's southern tributaries arise, and in the Rio Negro and Orinoco watershed, drainage is not sufficiently determinate to prevent extensive flooding in the wet season, so that large areas of marshland have developed. In parts of Central and East Africa, where the tilting of the plateaux surfaces following the formation of the Great Rift Valleys in the Pleistocene reversed some drainage patterns, extensive marshlands have developed, for example in Uganda around Lake Kyoga, and in Botswana where the unique inland delta of the Okavango developed.

The importance of wetlands of all kinds in the biogeochemical cycles of the world, in particular their function in trapping nitrogen washed from soils, is demonstrated in Figure 4.2. In the conversion of many of these marshland bogs and fens to agriculture, their function as traps for mineral elements is lost and the possibility of returning elements 'uphill' via bird populations is diminished. Many ecologists have pointed out the dangers of losing these ecologically important environments and some conservation schemes have been highly successful, such as, for example, the preservation of the extensive tracts of swampland in Florida for their tourist potential.

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17

Arctic and alpine tundra

17.1 Vegetation types

Arctic tundra and high alpine vegetation are complex mosaics of very different communities, each fragment being related to the local microclimate and to soil type. Arctic tundra is more varied than high-altitude tundra, with many communities intergrading in an intricate fashion, and some of these are set out in Table 17.1. The proportion of ground covered by each type varies latitudinally between low, middle and high Arctic, but everywhere it is the influence of local habitat variations that is paramount in determining the community patterns. The ecotone from forest to tundra is rarely abrupt and outliers of forest trees may occur on well drained sites to considerable distances beyond the forest edge – stunted white or black spruce (tamarack) in Canada, Dahurian larch in Siberia and the low birch, *Betula odorata*, in Scandinavia.

In contrast with the Arctic, the islands surrounding the Antarctic continent are treeless to much lower latitudes. Islands far distant from the continent may carry a vegetation whose physiognomy closely resembles tundra, although the two flora bear little relation to each other. Their resemblance is an excellent example of convergent evolution under extreme habitat conditions.

In middle latitudes, the alpine stages on high mountains are comparable in many ways, floristically and physiognomically, to the vegetation near sea level in the low Arctic, and there are many common species represented as latitudinal ecotypes. For example, the more impoverished alpine floras of Norway are so nearly identical to the more extreme tundra habitats of south-east Greenland that they must be regarded as the same formation. It is only at the racial level that the differentiation can be detected. More mesic habitats in Greenland are much less comparable. However, important differences in energy conditions and other factors at work in the two ecosystems make direct comparison impossible. For example, primary production in alpine sites is probably less than half that of the low

Table 17.1 The major arctic and alpine physiognomic types.

	Typology	Vegetation
arctic tundra	mesophilous types on well drained sites	sward: sedges and grasses (15–30 cm), various forbs and under-shrubs, mosses and lichens
		heathlands: dominated by ericaceans and *Vaccinium* spp.; sites often related to snow patches
		shrub tundra: may often reach over 1 m, especially along rivers and lakesides
	hygrophilous types on impeded drainage sites	hummocky tundra: cotton grass (*Eriophorium* spp.), sedges, grasses, *Sphagnum* spp. and other mosses with many forbs
		shrub tundra: dwarf willows and alders with herbs similar to hummocky tundra
	xerophilous types on morainic material	lichens with xerophilous herbs, e.g. rock sedge (*Carex rupestris*)
		shrub tundra: dwarf birches and willows
	barrens and fell fields, less than 50% plant cover	
alpine tundra		rocky site associations: compact Chamaephytes and Hemicryptophytes
		meadows: grasses, sedges, forbs and under-shrubs

Forbs are flowering herbs other than grasses and sedges. The terms 'Chamaephyte' and 'Hemicryptophyte' are derived from Runkiaer's classification (see Table 1.1). In the Arctic on rocky sites near permanent ice caps there are many lichen-free areas now identified as the result of the 'Little Ice Age' (see Chapter 8).

Arctic tundra. Moreover, data for energy and moisture balance and for ultraviolet and cosmic radiation indicate that these environments 'undergo one of the greatest energy fluctuations observed on this planet' (Terjung *et al.* 1969). However, the large number of forms peculiar to the alpine stage means that this formation is richer floristically than the arctic tundra.

Low-latitude mountains may also have an alpine stage that in some cases resembles tundra, being composed of low herbaceous perennials, and arctic genera may be present, but there are few arctic species. The low-latitude high mountains have in addition vegetation types not present in the Arctic or mid-latitudes, for example, the sentinel-like *Senecios* and *Lobelias* of the African volcanoes and the

tall grasslands with woody shrubs of many well watered tropical mountains.

Experimental work on high-latitude and high-altitude plants has demonstrated that the effect of ultraviolet radiation on the latter is an important selective factor in the generation of ecotypes in arctic–alpine species (Robberecht *et al.* 1980). It has been known for some time that enhanced ultraviolet (UV) radiation depresses the rate of photosynthesis and restricts leaf growth in some mid-latitude species (Sissons & Caldwell 1975). The intensity of solar radiation in the UV-B wavelength range (280–320 nm) increases equatorwards with increasing altitude. Thus, at low latitude and high elevations it is seven-fold greater than at sea level in the Arctic and has significant selective effects. These have now been demonstrated in the species *Oxyria digyna*, whose Arctic and Alpine ecotypes show inherent qualitative and quantitative differences in their UV radiation sensitivity. In the arctic form, several photosynthetic pathways are damaged by UV radiation, whereas the alpine form is resistant. Moreover, the optical properties of leaves of the alpine forms of a number of species tested in Venezuela, Peru and Hawaii are such that a transmittance of UV radiation of only 2% is consistently reported. The arctic forms of these species, on the other hand, show variable transmittance when tested at sea level in the Arctic region.

17.2   Biomass, production and mineral cycles

The range of plant biomass in arctic tundra is very wide; for example, shrub tundra measured at 63°N 168°E gave a figure of 14.3 t ha^{-1}, but tundra with similar physiognomy measured at 75°N 140°E yielded only 3.4 t ha^{-1}. As in desert communities, life is maintained more easily underground and proportions of underground organs are usually 80% or more of the flowering plant biomass. Most communities contain significant proportions of non-flowering plants (mosses and lichens): in the first example above, about 8–9% of the plant biomass comprises non-flowering plants, and, in the second example about 18%. As might be expected, the totals of dead material are usually large (Fig. 15.2), both above and below ground, in waterlogged conditions often comprising more than 70% of the total organic matter. There are few figures for production in these ecosystem types. Figures from the low Arctic of Canada, north-eastern Siberia and Sweden range between 250 and 1800 kg ha^{-1} y^{-1}. Alpine tundras

of temperate latitudes yield sample figures usually between 100 and $1000 \, \text{kg} \, \text{ha}^{-1} \, \text{y}^{-1}$.

The mineral cycles in high-latitude tundra are unique in being dominated by nitrogen, and this element alone almost outweighs the total of all the other elements cycled in both shrub and herbaceous tundra.

17.3   Tundra soils

The soils of these lands reflect the almost universal waterlogging, short 'warm' periods, reserves of cold, infrequent aeration and low rates of weathering and mineralization in the frequent *gleying* that occurs and the mass of peat that is usual. A gley horizon is typically blue-grey or grey with rusty brown streaks and mottling, the latter produced by poor aeration and the conversion of ferrous salts to some form of ferric oxide. In grassy and flowering tundra with relatively large amounts of litterfall, greater amounts of cations are supplied to the soil than in shrub tundra. This, plus lower humidity and the better aeration usual in such communities, ensures higher rates of decomposition, and these soils carry a higher soil animal population, even including earthworms. In practically all the main tundra types, alpine and arctic, a major role in soil restructuring and mineral cycling is played by rodents, except where permafrost lies near the surface. The ability of rodent populations to consume large quantities of organic matter above and below ground is surprising. For example, in one alpine ecosystem studied in the Rockies, over half the total annual net primary production is consumed by ground squirrels.

17.4   The origin of the arctic tundra

Clearly only a comparatively short time ago (approximately 10 000 years) extensive glaciers covered large areas of the present location of this formation-type. Were there during the last glacial epoch equivalent extensive tundra lands fringing the ice caps? Although characteristic tundra landscape features can be found in former periglacial areas like East Anglia – stone polygons, stone stripes and solifluction deposits, for example – fossil evidence seems to suggest that over most of Eurasia, at any rate, tundra was destroyed and re-evolved several times during the Quaternary. During the warmest intergla-

cials, forest seems to have extended well into the Arctic circle itself. In fact, the extensive tundra lands of today seem to be an exception to the pattern of the last two or three interglacials.

17.5　Man and the tundra lands

Low productivity and a harsh climate have inevitably restricted man's use of these lands. The cultures that evolved in the past were adapted to the ecosystem's severe cycle of abundance and scarcity and are now almost completely degraded by the extension of industrialized cultures. Efforts in Canada and Sweden to offset the breakdown of the ecological pattern of the indigenous peoples by increasing the saleable product from the area have met with only limited success. In Canada, for example, the problems of the domestication of the musk-ox have largely been overcome, although as yet production of its fine wool is practically confined to the experimental station. In Sweden, the Lapps have turned to exporting reindeer meat and hides, but only where they are able to follow their traditional way of life. However, in all these Arctic lands the greatest threat is not from lack of product but from the demand for labour for mines. It is an accident of geography that these lands coincide with richly mineralized rocks, and mines and smelters with their needs of labour and road, rail and pipeline communications open up large tracts of country to poorly controlled development and tourist activity. (See Lawson (1987) for details of damage from pipeline construction in Alaska.) Such difficulties are not confined to the Western world. In the USSR the release of large areas of State nature reserve to other users from 1951 onwards has had considerable impact on the natural ecosystems with the influx of urban populations serving the mines. (For a review of human effects on tundra vegetation, see Andreyer (1981).)

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18

The vegetation of estuaries and sea shores

The zone between the sea and the land is occupied by a diversity of ecosystem types developed over a variety of habitats – dunes, brackish lagoons, intertidal mud and sand flats – presented by the coastal zone. In spite of the difficulties presented by salinity, the inshore marine and estuarine habitats are some of the 'most naturally fertile in the world' (Odum 1963). There are several reasons for this:

  (a) the rapid circulation of nutrients and food promoted by tidal action;
  (b) the trapping of nutrients both physically in mud-derived land and biologically by direct extraction from continually stirred sea water, a process in which both animals and plants participate;
  (c) the often more equable local climatic conditions; and
  (d) the close contact between stages of the food chain.

There is not sufficient space in this book to describe even in outline all the varieties of coastal vegetation types, but the student will find a good account in Polunin and Walters (1985). The present account is confined to a brief examination of the implications of human use of the ecosystems, as they are a model for the increasing conflict between short-term need and long-term conservation that afflicts almost every vegetation type.

The functions of coastal vegetation around the world in relation to human need are various, and in many places of great importance. We can summarize the two most important aspects as follows:

  (a) the extension of the land surface, which may be used for agriculture after suitable treatment; and
  (b) the protection of lowland from the effects of storm damage.

We shall now look at these two aspects in more detail.

18.1 Extension of the land surface

This process is particularly important in some of the world's great deltas – the Ganges, the Amazon, the Irrawaddy, the Mekong and so on. The mud that is trapped is usually nutrient-rich, and in tropical and subtropical lands it produces some remarkably high figures for net primary production. For example, in South Vietnam, net primary production with new 'high-yield' varieties of rice reaches $20t$ ha^{-1} y^{-1}, and in Java, coastal sugar-cane plantations on former mangrove swamps have one of the highest net primary productions ever recorded at $94t$ ha^{-1} y^{-1}, which is very near the theoretical potential photosynthetic limits (see Fig. 3.5).

In the tropical world generally, the most important agents in this extension of the land are the mangroves (Fig. 18.1). Although not entirely confined to the tropics – they occur in the Gulf of Aqaba, South Africa and New Zealand – the 20 species or so that make up this highly adapted vegetation spread throughout the tropical world on low, muddy shores and are extraordinarily effective in extending the land surface. Their effectiveness is enhanced by differentiation of niche amongst the species, some preferring sandy substrates, some muddy conditions, and by the degree of salinity they can tolerate. All possess a form of specialized breathing apparatus (*pneumatophores*) and can develop stilt roots. They are usually not present where strong wave action is likely.

In *Sonneratia*, for example, the pneumatophores are vertical post-like organs containing fine pores that allow the passage of air at low tide but not water at high tide. Some, for example the red mangrove (*Rhizophora mangle*), have a form of viviparous reproduction, the primary root of the seedling bursting through the hanging fruit as a slender dark-like structure while still carried on the parent tree. The seedling may drop from the parent plant, directly penetrating the mud, and produce lateral roots in a matter of hours, or, if shed at high tide, may be transported to a favourable location.

Semenuik (1985) has shown the link between the geomorphic units that have developed in northern Australia following the marine transgression of postglacial times and the mangrove community types within the overall climatic framework. Main tidal flat, hinterland fringe, alluvial fan, spit, tidal creek bank, tidal creek shoal and rocky shore all have distinctive mangrove communities.

The mangrove vegetation of the world as a whole is divided into two distinct phytogeographic regions. The floristically richer eastern mangrove zone extends from Australia along Asian shores to East
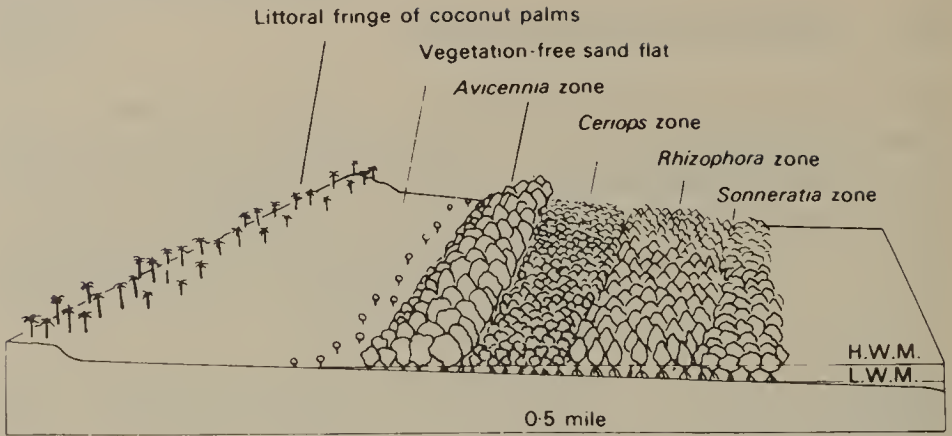
Figure 18.1   Zonation in mangrove swamps near Tanga, East Africa. (Data from Walter (1984).) Note that all mangrove species shown have stilt roots.

Africa. The western formation occupies coasts on the American continent and western Africa. Although the regions have similar composition in their genera, few species are shared between them.

Noisome though they may be, the mangrove swamp is a highly effective ally to human beings in protecting and extending the land and, where the mangrove forms tall forest on the landward side, it can be a valuable source of timber. In Malaya, for example, regular felling of mangrove forest on a 30-year rotation long provided construction timber, so much so that there is little climax left. However, mangrove can be easily damaged by pollution, especially those species which prefer brackish water. This seems to be happening in coastal Florida, and as industrialization proceeds along coasts and river basins the mangrove vegetation may be in great need of conservation.

In temperate parts of the world the function of stabilizing the muddy coasts is carried out by many species of saltmarsh herbs. These too can be highly effective in increasing the land surface, and the frequent muddy creeks and tidal pools in both temperate and tropical lands have an important role to play in inshore fisheries, as they often form the nursery for fish that are later harvested at sea.

The growth and development of salt marshes is one of the most striking examples of the process of plant succession in nature. One of its most notable features is the geomorphological changes that result from the trapping of tidal mud by growing plants. The initial surface is usually a mud bank carrying marine algae, which, by deposition, has reached a sufficient height to be exposed at low water long enough for specialized plants to take root. The first plants to appear

are obligate halophytes such as *Salicornia* spp. or plants such as *Spartina townsendii*. The length of exposure of the surface can be very critical for these plants. For example, *Salicornia europeae* needs at least three days for its roots to become sufficiently long for it to withstand tidal scour. Once established, further mud is trapped by the plants and the surface begins to grow upwards. At this stage, although the marsh will still be covered at high tide, the first channels appear as water drains away at low tide. The increased efficiency of drainage that the channels provide at the landward edge of the marsh allows the entry of further species, for example *Halimione portucaloides* along the channels themselves and *Glyceria maritima* higher up the marsh. As the plants on the higher side trap further materials, the salt marsh begins to be significantly divided into upper emergent and lower submergent areas. The divide between the two is around mean high-water mark. Both upper and lower marshes are inundated but the frequency is significantly different between the two areas. On the whole, apart from storms, only the high spring tides cover the upper marsh, usually for less than 1 h in daylight and less than 360 times during the year. The lower marsh, however, is inundated more than 360 times annually, the average daylight submergence being over 1.2 h.

As more plants move in, for example woody perennials such as *Armeria maritima* and *Limonium vulgaris*, and the surface continues to elevate, the channels deepen and some of the early minor tributaries may be cut off as erosion by scour undercuts the banks, causing their collapse. These blocked channels may be left as bare salt pans, which, as water evaporates, acquire salinities well beyond the tolerance levels of the marsh plants. Thus, colonization may be very slow or may not take place at all.

By the latest stages of marsh development only the highest spring tides may cover the whole surface and plants such as *Juncus maritimus* and *Festuca rubra* may be added.

Apart from *Spartina* and the later grasses, the plants that colonize this environment are nearly all from two families, the Plumbaginaceae and Chenopodiaceae. This is a clear indication of the degree of difficulty of this habitat. Plants have to possess physiological adaptations not only to salinity but also to very poor root aeration. Some of the former adaptations have been indicated previously (Ch. 6), but not a great deal is known of how the latter is overcome. When it is considered that the soil atmospheric oxygen content can fall to as little as 1–2% and the carbon dioxide level can rise to as much as 4%, it can be seen that the problem is almost as formidable as that posed

by salinity. As is the case with adaptations to high salinity, it is probable that more than one solution will be involved.

Although all saltmarsh plants must perforce be adapted to the extreme chemical conditions of their habitat, this does not mean that their distribution within the community is entirely a function of this factor. As in more 'normal' communities, competition, predation and physical disturbance still play a part in determining the details of community structure. For example, in New England salt marshes Bertness and Ellison (1987) show that the upper marsh in their study area is dominated by *Spartina patens* and *Juncus gerardi*, whereas the lower marsh is dominated by *Spartina alterniflora*. However, they demonstrate by experiment that the last species is perfectly capable of vigorous growth in the upper marsh but is excluded by competition. Also, they show that the detailed distribution of *Salicornia* spp. at the seaward edge of the marsh is a function of predation especially.

18.2   Protection of lowland

This role is particularly fulfilled by sand dunes stabilized initially by grasses. Most of these, like the marram grass, are highly xeromorphic and adapted in their rooting to take advantage of fresh sand by springing strong lateral roots into the sand as it is built up. In the succession on dunes, they may be followed by xeromorphic woody plants that can take advantage of the nutrients bonded into the humus created by the dead remains of the grasses. In many temperate lands, people have taken advantage of the stabilized sandy habitats and planted pines, for example in the Landes of France and along the western coast of Jutland in Denmark.

The protective value of the dunes is incalculable. For example, along the southern North Sea from northern Denmark to Cap Gris Nez, they protect densely populated lowland on former salt marshes behind them. When this barrier has been penetrated, as in the great flooding of the 12th century, which created the Zuider Zee, and again in 1953, its natural protection has had to be replaced by a series of artificial barriers constructed at great cost.

Doing (1985) has examined the coastal sand dunes in various parts of the world and provided a clear biogeographical exposition of their varieties. Broadly, coastal dune landscapes can be divided into those of tropical and subtropical coasts and those of temperate and cold coasts. The former can be subdivided into humid and arid types, the latter into cool–temperate and boreal to sub-Arctic types. Doing
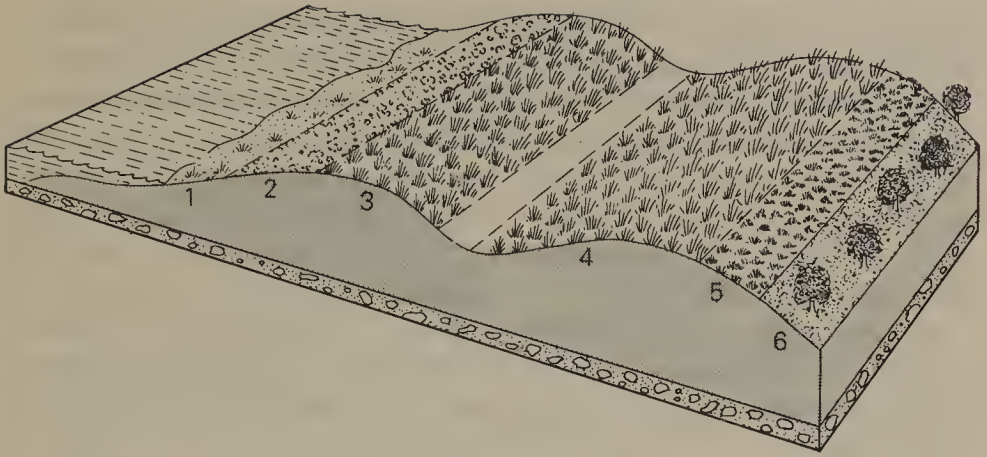
Figure 18.2 Typical dune development in mid-latitudes. (Data from Doing (1985).) Vegetation example from dunes near Cap Gris Nez, France: (1) ephemeral tidemark communities *(Calcile maritima)*; (2) perennial tidemark communities (*Hankenia peploides*); (3) embryonic dune or frontal ridge (*Agropyron junceiforma*), minor part of sand fixed by vegetation; (4) central fore-dune ridge (*Ammophila cuenaria*), major part of sand fixed by vegetation; (5) sheltered zone (*Festuca rubra grenaria*), accretion of a few decimetres of sand per year; (6) pioneer communities in stabilized areas (*Torula ruralis* plus woody invaders), accretion of a few centimetres of sand per year. Note: zones 1–4 = yellow dune type; zones 5 and 6 = grey dune type.

suggests that dune coasts of all kinds tend to follow a single model of lower front ridge and higher inner ridge, with a distinctive zonation from tidal edge to the inner-ridge landward slope. Where dune landscapes are complex and divert from this model, they will do so especially where disturbance by the wind is not balanced by the sand fixation rate by plants. The model and zonation are shown in Figure 18.2.

Tropical–humid coastal dunes are generally lower than those in arid areas and lower than cool–temperate dunes. The last are also higher than those in cold regions and are particularly extensive and well developed on the temperate coasts of the Northern Hemisphere. Temperate dunes in Australia, in contrast, have a stronger resemblance to humid–tropical dunes, with grasses and shrubs dominating the dune ridges. Spinifex is abundant in the outer dune and woody *Acacia* species dominate the inner ridge. In temperate lands, virtually all the herbaceous species are winter annuals.

The zonation indicated in Figure 18.2 is not a rigid one and plants of one zone may intergrade with others. For example, Watkinson (1985) showed that *Calkile edertuda*, a species of the seaward edge, appears most abundantly in that zone but also occurs with decreasing frequency through the dune habitat towards the land. The author

demonstrates that the gradient of frequency landward is only main-
tained by a constant supply of seeds from the seaward population.

Tropical sand dunes in humid regions have mainly low grasses
(*Sporobolus* spp.) in the front ridge and woody species in the second
ridge. However, the fore dune in many areas is colonized by woody
species, for example, *Casuarina* spp., *Ipomoea pes-caprae* and
Scaevola taccada in south-east Asia. Some of the major species also
occur in saltmarsh habitats.

In arid regions, dune species are either halophytic taxa (*Suaeda*,
Tamarix, *Frankenia*, etc.) or grasses, which also occur in non-coastal
dunes (*Aristeda* etc.). The inner dunes are usually high, with little or
no vegetation.

Cold environments (boreal and sub-Arctic regions) usually have
low dunes, with *Elymus* as the main dune-building species, and there
is a range of intermediate forms between various types of tidemark
and dune ecosystem.

On barrier islands along flat coasts, especially where hurricanes
occur frequently, for example the Outer Banks of North Carolina,
the fore dune remains low owing to 'overwash' by the sea. This
creates a special type of habitat associated in this particular instance
with *Spartina patens*.

The distinction between 'yellow' and 'grey' dunes suggested in
Doing's model (Fig. 18.2) is that between active, sand-accreting
zones (1–4) and sheltered, stabilized zones (5 and 6).

Any demand for usage of the coastline that increases its commer-
cial value is likely to damage the very ecosystem that protects us at so
little expense. In the USA, for example, the eastern seaboard
marshes from New Jersey southwards are the scene of a fierce
struggle between developers and conservationists, not only over
development, but also over coastal pollution. In Europe, the dune
coasts with their sandy beaches are under pressure, particularly, from
leisure demands. Trampling by children and adults can do
tremendous damage to the delicate balance of growth on dune land.
Although in Britain most local authorities are aware of this damage
and attempt to protect dunes, the pressure for access is always there.
The estuaries, which are the nurseries of so much valuable fish, are
almost everywhere suffering from pollution, much of which could be
avoided, given sufficient political determination by private industry
and public bodies to face the costs. As Odum (1963) says, 'Conver-
sion of already useful estuaries into open sewers for industrial wastes
or into corn fields or house sites for which the topography is not well
suited, is not in the best interests of man.'

Coastal vegetation is most certainly one case where the estimate of economic benefits derived from the ecosystem can be assessed in terms for once acceptable to the cost–benefit analyst. Unfortunately, the exercise is rarely attempted and there are few models available to do this.

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Conclusion

Throughout the last two parts of this book the reader will have noted that, in practically every major ecosystem type from the tundra to the tropical rainforests, the addition of new knowledge is increasing the ability of human beings to bring vast tracts of the Earth's surface into a managed rather than a wild state. The progress of conservation of our great natural heritage of plants and soils is slow and uncertain, but it is undoubtedly one of the most important tasks (if not *the* most important) of the next few decades. With the world's population expected to double by the first decade of the next century, the need for the basic ecological and biogeographical information on which to base rational policies is urgent. The author hopes that the information provided in this book will enable its readers to participate more effectively in the process of policy-making, either as future conservationists themselves or as informed persons without whom no rational policies can succeed.

Glossary

anaerobic	Without free oxygen.
anion	Negatively charged particle (non-metallic) in solution.
association	Part of a plant formation dominated by a characteristic species.
autotroph	A plant able to feed itself, i.e. provide its own energy supply.
biomass	The weight of living organisms in an ecosystem. Can be measured as living (fresh) weight, dry weight, organic matter (i.e. ash-free) weight, weight of carbon, units of heat and in various other ways.
biosphere	That part of the Earth in which ecosystems can operate.
catena	Chain of soil types from top to bottom of a slope.
cation	Positively charged particle (metals and hydrogen) in solution.
clay–humus complex	The electrically linked mass of clay and humus (colloidal) molecules in soil.
colloids	Substances present in solution where molecules group together to form solute particles. The substances can exist in a mobile (sol) state or in a stable state (gel).
community	The plants and animals that compose the living part of an ecosystem.
diurnal	Relating to daily events.
dominant	A plant that because of its coverage above ground or the root space it occupies below ground controls or modifies the immediate environment and determines the conditions of life for other members of the community.
ecosystem	The complex of the living community and the non-living environment that it inhabits functioning as an integrated system.
ecotone	A zone of transition between two distinct plant communities.

ecotype	A group of local populations within a species from the same type of environment genetically specialized for that environment. (Also called ecological races.)
endemic	A plant (or animal) restricted to a relatively small geographic area or habitat.
epiphyte	A plant that uses another plant for physical support but without roots in the ground. Epiphytes take no water or other nutrients from the supporting plant.
eutrophic	Well supplied with nutrients.
evapotranspiration	The combined loss of water to the atmosphere from a land surface and its plant cover.
flora	All the kinds of plants that make up the vegetation of an area.
formation	A distinct part of a formation-type identifiable geographically.
formation-type	A world vegetation type recognized by its dominance overall by plants of the same life-form.
genotype	The gene content of an organism.
guttation	The exudation of water as a liquid by plant leaves.
heterotroph	Plant (or animal) that utilizes food created by autotrophs.
holocoenotic	Wholly unified. Referring to ecosystem components both living and non-living.
horizon	Distinct soil layer.
lapse rate	The rate at which temperature falls with increasing height. Dry adiabatic lapse rate is the rate at which temperature falls in rising air.
leaching	The removal of dissolved or suspended materials by water percolating downwards.
life-form	A distinctive set of shape, size and other characteristics of morphology shared by a group of related or unrelated species.
limiting factor	Any factor that checks potential growth in an ecosystem.
meiosis	Reduction division when gametes are formed. Chromosome numbers in each gamete are half the total (haploid) of those in somatic cells (diploid).
mutation	A change in the inheritable characteristics of a living thing.

mycorrhizae	Fungi inhabiting the roots of vascular plants.
Neolithic	The period of human prehistory following the adoption of an agricultural way of life but before the introduction of metal tools.
niche	The role an organism plays in an ecosystem.
nutrient	Any element or compound essential to life.
oligotrophic	Low in nutrients.
Palaeolithic	The period of human prehistory in which stone tools were used and before the introduction of agriculture. Many authorities recognize the increasing technological sophistication of the later Palaeolithic as the Mesolithic.
phenecotype	A population that is adapted to its local environment by physiological response but not by genetic changes.
phenetic	Refers to all the features of an organism.
phenology	The study of flowering, leafing, growth rate, etc., that occur periodically in response to environmental rhythms.
phenotype	The expression of the genotype of a population or an organism interacting with the environment.
photoperiod	Length of daytime in which light is available.
phylogenetic	Relating to the evolutionary history of an organism.
primary production	Total amount of organic matter including that used by plant respiration during a period of measurement. Also called gross primary production. Net primary production is the organic matter stored in plant tissues in excess of respiration during a period of measurement. In relation to vegetation both figures are usually given as mean weights per unit area.
profile	The arrangement of soil horizons from surface to bedrock.
radiation	Emission and transmission of energy in wave form, applied to both electromagnetic energy and particles from radioactive substances.
sere	A series of plant communities that successively occupy the same piece of ground.
synusia	A set of plants within a complex community that share the same life-form.
transpiration	The process of water-vapour release to the atmosphere from the above-ground parts of plants.

valency   Combining power of an atom (measured as the number of hydrogen atoms that an atom will combine with or replace).

zonal vegetation   A broadly conceived vegetation unit that occupies a larger part of the surface in areas without significant human ecological effects and is dominated by the macroclimatic characteristics. (Azonal vegetation is that dominated by extreme soil characteristics.)

Index of Subjects

Index of Countries and Major Regions in Text

Index of Plant Common Names

Where botanical name only is used page number is italicised.

Building on a highly successful first edition, this thoroughly revised and expanded text offers a detailed but concise description of a wide range of concepts and topics in the field of vegetation ecology. The material provides an ideal introduction to an area of study which occupies a prominent position in ecology, geography and biogeography.

Chapter 1 has been developed considerably to take greater account of plant classification and evolution, including cladistics. This section has also been expanded to offer a fuller appreciation of plant life forms. Fossil records often provide much valuable information on the historical patterns of plant distributions and Chapter 2 deals with this evidence, adopting an increased emphasis on the geological aspects of the topic. Energy variation in relation to ecology/biogeography and ecological physiology are examined in Chapters 3 and 4. A wide diversity of environmental factors such as temperature, mineral cycles and ionic content of soils can have profound effects on the distribution of plants. Chapters 5 and 6 highlight the relationships between ecosystem conditions and plant distribution and Chapter 7 investigates the analysis, classification and mapping of plant communities.

Chapter 8 marks the beginning of the second part of the book which focuses on the patterns of world vegetation. The examination of tropical areas includes a fresh look at savanna regions while the deciduous and coniferous forests, which form an important part of the biosphere, are described with particular attention to productivity, mineral cycles and community arrangements. An amazing biological feature of plants is their ability to adapt to some of the harshest conditions, and the final chapter takes a close look at plants living in extreme habitats.

The illustrations have been carefully tailored to provide the optimal b̶ for approachable form. The author has succeeded in producing a valuable introductory text on vegetational ecology for students of biogeography, environmental science, geography and ecology.